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A REVISION OF THE ESTUARINE CRAB GENUS *ILYOGRAPSUS* BARNARD, 1955 (CRUSTACEA: DECAPODA: BRACHYURA: MACROPHTHALMIDAE), WITH DESCRIPTIONS OF A NEW GENUS AND ONE NEW SPECIES

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ABSTRACT. **–** The taxonomy of the poorly known estuarine crab genus *Ilyograpsus* Barnard, 1955, is revised. Five species are recognized in the genus: *I. paludicola* (Rathbun, 1909) from Southeast to South Asia, northeastern Australia and New Caledonia; *I. rhizophorae* Barnard, 1955 (type species) from the Red Sea and the western Indian Ocean; *I. nodulosus* Sakai, 1983, from southern Japan; *I. vannini* Sawada, Hosogi & Sakai, 2005 from Somalia; and *I. daviei*, new species, from Queensland, Australia. The four previously described species are rediagnosed. A new genus, *Apograpsus*, is established for the recently described species *Ilyograpsus paantu* Naruse & Kishino, 2006. The two genera are referred to the family Macrophthalmidae. Affinities of the two genera to *Enigmaplax* Davie, 1993 and a hypothetical ancestor of *Macrophthalmus* proposed by Barnes (1967) are discussed.

KEY WORDS. **–** Crustacea, Decapoda, Brachyura, Macrophthalmidae, *Ilyograpsus*, new species, new genus, Indo-West Pacific.

INTRODUCTION

The peculiar crab genus *Ilyograpsus* Barnard, 1955, is currently represented by five described species, *I. paludicola* (Rathbun, 1909), *I. rhizophorae* Barnard, 1955, *I. nodulosus* Sakai, 1983, *I. vannini* Sawada, Hosogi & Sakai, 2005, and *I. paantu* Naruse & Kishino, 2006. The first species, *I. paludicola*, was described on the basis of a female specimen from the Gulf of Thailand, and it was originally assigned to the genus *Camptandrium* Stimpson, 1858. Rathbun (1909) highlighted the resemblance between her new species and *Camptandrium sexdentatum* Stimpson, 1858. The genus *Camptandrium* Stimpson, 1858, is currently classified in the family Camptandriidae Stimpson, 1858 (see Tan & Ng, 1999). The second species, *Ilyograpsus rhizophorae*, is the type species of the genus, described on the basis of a single male specimen collected from mangrove swamps in Inhambane, Mozambique, East Africa. Barnard (1955) commented on the very close resemblance between *I. rhizophorae* and *Camptandrium paludicola*, although he referred *Ilyograpsus* to the subfamily Grapsinae of the family Grapsidae. Tesch (1918) had earlier remarked that *Camptandrium paludicola* should be assigned to the genus *Cyrtograpsus* Dana, 1851, of the subfamily Varuninae of the same family, instead. Based on an examination of material from Madagascar, Crosnier (1965) concluded that *Ilyograpsus rhizophorae* and *Camptandrium paludicola* were conspecific, and the name *Ilyograpsus paludicola* should be used for that taxon. Sakai (1983) described *I. nodulosus* (as *nodulosa*) on the basis of a small specimen lacking any pereopods from Iriomote Island, Ryukyu Islands, as a second representative of the genus at that time. Sawada et al. (2005) briefly reviewed the genus. They reinstated *I. rhizophorae*, and described a new species, *I. vannini*, based on material from Somalia and Ethiopia. They considered that the records of *Ilyograpsus paludicola* from Madagascar (Crosnier, 1965) and the Sinai Peninsula (Holthuis, 1977) actually belonged to their new species, *I. vannini*. Naruse & Kishino (2006) recently described a distinctive new species *I. paantu* from the Ryukyu Islands of southern Japan. They also gave an account on *I. nodulosus* and briefly discussed the taxonomic position of the genus. Certainly, there have been many records of the genus as it is widespread in the Indo-West Pacific (e.g., Hartnoll, 1975; Yamaguchi et al., 1976, 1987; Sakai, 1983; Tirmizi et al., 1985; Tirmizi & Ghani, 1996; Kishino et al., 2001a, 2001b; Davie, 2002; Nakasone & Irei, 2003; Yeo et al., 2004), but most were referred to *I. paludicola*.

As is apparent from the above summary, the taxonomic position of the genus has been controversial. Fukuda (1978) first noted that *Ilyograpsus* was more likely to be an ocypodid on the basis of larval morphology. Cuesta et al. (1997) and Flores et al. (2003) supported Fukuda's (1978) view, also based on larval evidence. Števčić (2005), who recognized Macrophthalmidae, established a new tribe Ilyograpsini, together with the tribe Macrophthalmini. Naruse & Kishino (2006) also assigned *Ilyograpsus* to Macrophthalmidae, following Flores et al. (2003). Ng et al. (2008) regarded Ilyograpsini as a subfamily, Ilyograpsinae.

This study was initiated to identify material from estuarine environments in Tosa Bay, Kochi Prefecture, Japan, submitted to the senior author for identification by Prof. Y. Machida of the Faculty of Science, Kochi University. In the process attempting to identify the material from the existing literature, it quickly became apparent that the identities of *I. paludicola* and *I. nodulosus* are both central to the question at hand. In spite of the study by Sawada et al. (2005) and Naruse & Kishino (2006), there also remain uncertainties about the identity of *I. paludicola* and *I. rhizophorae*. In order to clarify the uncertainties in the taxonomy of species of the genus, we examined specimens from various localities in the Indo-West Pacific regions, including Japan, Vietnam, Malaysia, Singapore, Indonesia, Australia, New Caledonia and Madagascar, as well as the paratypes of *I. vannini* from Ethiopia. We came to a conclusion that the five previously described species are all valid, although it was found that the paratypes of *I. vannini* are actually *I. rhizophorae*. One new species, *I. daviei*, which had been misidentified with *I. paludicola*, is described from Queensland in Australia. A new genus, *Apograpsus*, is proposed for *I. paantu*. Affinities of the two genera are briefly discussed. We concur that *Ilyograpsus* and *Apograpsus* are members of the Macrophthalmidae.

MATERIALS AND METHODS

Specimens examined in this study are deposited in the following institutions: Muséum national d'Histoire naturelle, Paris, France (MNHN); Nationaal Naturhistorisch Museum, Leiden, the Netherlands (RMNH); Natural History Museum and Institute, Chiba, Japan (CBM); Osaka Museum of Natural History, Osaka, Japan (OMNH); Queensland Museum, Brisbane, Australia (QM); Ryukyu University Museum Fujyukan, Okinawa, Japan (RUMF); Shikoku Institute of Natural History, Susaki, Japan (SINH); Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC).

The carapace length is measured from the level of the anterior edges of the front to the midpoint of the posterodorsal margin of the carapace (Fig. 1). The carapace width is measured across the third or the second anterolateral tooth, representing the broadest position (Fig. 1). The size of specimens is indicated primarily by the carapace length (cl). Measurements of segments of the ambulatory legs are shown in Fig. 1. The measurements of the ambulatory legs were made in the case that legs were attached to the body or that identity of the legs could be reasonably estimated.

TAXONOMIC ACCOUNT

Macrophthalmidae Dana, 1851

Ilyograpsus Barnard, 1955

Ilyograpsus Barnard, 1955: 25; Crosnier, 1965: 31; Sawada et al., 2005: 852.

***Type species*. –** *Ilyograpsus rhizophorae* Barnard, 1955, by monotypy.

***Diagnosis.* –** Carapace flattened, slightly wider than long, suboctogonal in general outline; dorsal surface smooth or microscopically granular; lateral margin usually with 4 (rarely 5) teeth including external orbital tooth, second tooth usually blunt. Front not constricted basally, proximal width slightly greater than half of front-orbital width. Postfrontal ridges transverse, without long setae. Orbit large; lower orbital margin laterally with 3–5 lobules in males, entirely granular in females, mesial angle not markedly produced; small inner orbital tooth present. Ocular peduncle stout, just reaching or slightly overreaching external orbital tooth; cornea large. Antennules transverse or slightly oblique; basal segment inflated. Interantennular septum narrow. Antennae in orbital hiatus; flagellum long, reaching or overreaching cornea. Central region of epistome distinctly convex. Third maxillipeds (Fig. 5E) not completely closing buccal cavern; carpus inserted medially on anterior margin of merus; merus smaller than ischium, with lateral and mesial margins upturned on outer surface, anterolateral angle rounded; merus with sinuous mesial and concave lateral margins, external surface with shallow longitudinal sulcus mesial to midline; no setose ridge on external surface of merus-ischium; exopod slender, reaching anterolateral angle of merus, width about 0.3 times width of ischium; exopodal flagellum well developed. Merus of cheliped not markedly narrowed distally, usually with small subdistal spine on dorsal margin; carpus without prominent tooth or spine on inner surface; fingers spoon-shaped at tips, not crossing when closed. Merus of male cheliped with or without prominent short crest on inner margin; dactylus with or without differentiated tooth on cutting edge. Ambulatory legs slender to moderately stout; meri not markedly tapering distally, each with sharp subdistal spine on anterior margin; propodi each with sharp tooth at each posterodistal angle; dactyli long, weakly curved, slightly compressed laterally, unarmed. Pleon of male (Fig. 3D) not occupying entire space between last pair of ambulatory legs, consisting of 7 free somites including telson; no medial constrictions; second somite with angular lateral margins; third somite weakly expanded laterally; third to sixth somites subequal in length, evenly tapering; telson longer than other somites, rounded terminally. Pleon of female (Fig. 5D) broadly rounded; fourth segments somite broadest; telson roundly triangular. First gonopod slightly curved, not constricted. Female gonopores some distance from suture between fifth and sixth sternites.

***Remarks.* –** *Ilyograpsus* Barnard, 1955, has been generally assigned to the family Grapsidae (Barnard, 1955; Crosnier,

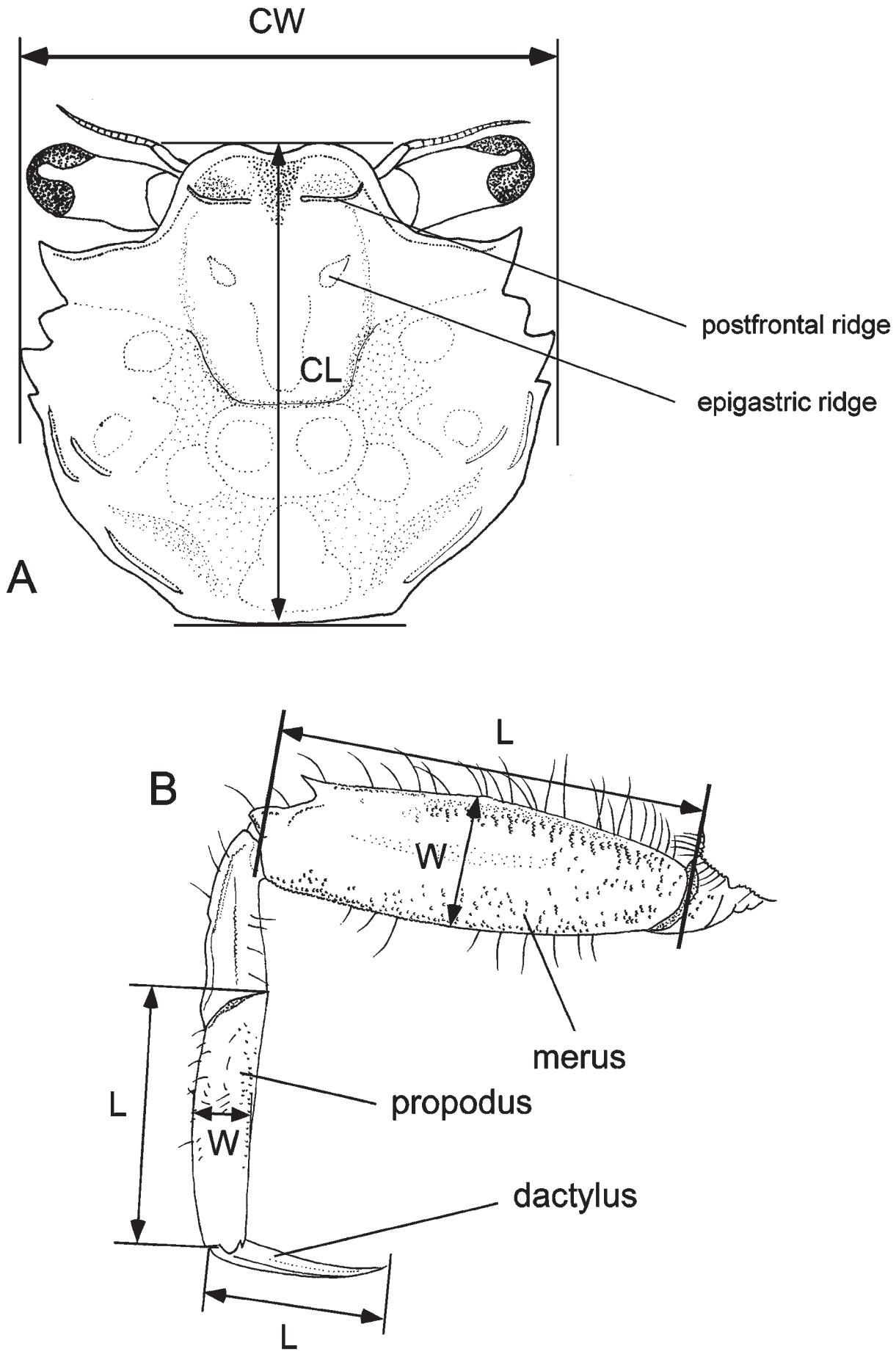

Fig. 1. Schematic illustrations of: A, carapace; B, ambulatory leg, showing measurements and terminology. CL, carapace length; CW, carapace width; L, length; W, width.

1965; Takeda & Nunomura, 1976; Yamaguchi et al., 1976; 1987; Sakai, 1983; Yeo et al., 2004), although the subfamilial assignment has been a subject of some disagreement, i.e., Varuninae (e.g., Yeo et al., 2004) or Grapsinae (e.g., Barnard, 1955; Crosnier, 1965). On the other hand, other authors cast doubt on the assignment of the genus to the Grapsidae sensu lato Fukuda (1978) and Flores et al. (2003) showed that the larval morphology of what they regarded as "*Ilyograpsus paludicola*" (these authors probably dealing with two separate species; see ***Remarks*** under the account of *I. paludicola*) is similar to that of *Macrophthalmus*, which has been referred to the subfamily Macrophthalminae Dana, 1851, family Ocypodidae Rafinesque, 1815. Naruse & Kishino (2006) also highlighted similarities in adult morphology between *Ilyograpsus* and *Macrophthalmus*, and they placed *Ilyograpsus* in the family Macrophthalmidae, following the recent trend in raising of all ocypodid subfamilies to full family status (Kitaura et al., 2002; Števčić, 2005; Schubart et al., 2006).

During this study, we also noticed that *Ilyograpsus* sensu stricto is morphologically very similar to *Enigmaplax* Davie, 1993, a monotypic genus (type species *E. littoralis* Davie, 1993) also originally placed in the Macrophthalminae (now Macrophthalmidae). Shared characters include: (1) the relatively wide orbit which is subequal to the width of the front and which accommodates the large ocular peduncle; (2) the presence of distinct postfrontal ridges; (3) a convex epistomal margin; (4) the third maxilliped with a merus which is smaller than the ischium; (5) the presence of a sharp subdistal spine on the dorsal margin of each ambulatory merus; and (6) the structure of the male pleon and gonopods (cf. Davie, 1993). It should be noted that the last two characters are also found in species of *Macrophthalmus* (personal observation). As well as *Enigmaplax*, *Ilyograpsus* agrees on most points with the hypothesized ancestral *Macrophthalmus* of Barnes (1967). The main points of differences are that the merus of the third maxilliped is smaller than the ischium as opposed to subequal; and the epistome has a convex central margin, not straight.

Main differences between *Ilyograpsus* and *Enigmaplax* are as follow. The general contour of the carapace is suboctogonal in *Ilyograpsus*, rather than quadrate in *Enigmaplax*. The lateral margin is armed with four teeth (including the external orbital tooth), rather than three in *Enigmaplax*. Furthermore, the fingers of the chela are spoon-shaped in *Ilyograpsus*, whereas they are pointed distally and cross each other in *Enigmaplax*. *Ilyograpsus* appears characteristic among macrophthalmids in having four anterolateral teeth, of which the second is always blunt. Most of other macrophthalmid species have two or three anterolateral teeth, except *M. philippinensis* Serène, 1971, *M. leptophthalmus* (H. Milne Edwards, 1852) and *M. latreillei* (Desmarest, 1822), which have four anterolateral teeth (Barnes, 1967, 1977).

Our study shows that the recently described *Ilyograpsus paantu* is quite distinctive, and the inclusion of it in the genus complicates the generic diagnosis of *Ilyograpsus*. In fact, we could not identify any possible synapomorphy between *I. paantu* and other species of *Ilyograpsus* when compared with other macrophthalmid genera. Therefore, we propose a new genus to accommodate *I. paantu* (see ***Remarks*** under the account of *Apograpsus*, new genus). As a result, the family Macrophthalmidae now comprises of five genera, *Macrophthalmus* Desmarest, 1823, *Australoplax* Barnes, 1966, *Enigmaplax* Davie, 1993, *Ilyograpsus* Barnard, 1955, and *Apograpsus*, new genus.

As mentioned before, Ng et al. (2008) recognized two subfamilies within Macrophthamidae, Macrophthaminae and Ilyograsinae, raising the tribes proposed by Števčić (2005). We feel doubt in recognizing such a subfamilial division, because of the close similarities between *Ilyograpsus* and *Enigmaplax*, of which the latter is assigned to Macrophthaminae. Our morphological comparison seems to suggest that *Ilyograpsus* is rather basal within Macrophthamidae. In this study, we do not maintain the subfamilial classification.

Other than the characters relating to the cheliped, pleon and pleonal appendages, the following differences may be related to sexual dimorphism in *llyograpsus*: the regions of the carapace is more distinctly defined in males than in females; the lower orbital margin is provided with three or four differentiated lobules laterally in males, whereas it is lined with minute to small granules or nearly smooth in females; and the ambulatory legs are relatively longer and more slender in males than in females. Therefore, only comparisons of specimens of the similar sex are effective for species recognition.

Sawada et al. (2005) and Naruse & Kishino (2006) cited several characters for species discrimination (e.g., condition of the dorsal carapace surface, arrangement of the anterolateral teeth of the carapace, ornamentation of the cheliped merus, and structure of the first gonopod). However, our study, using more extensive material, suggests that some of them are not always reliable because of individual or ontogenetic variability. For example, the degree of the dorsal sculpture on the carapace is substantially different between males and females in *I. paludicola* and *I. nodulosus*. The dentition of the fingers of the chelipeds is considerably more variable between different sexes and between different growth stages in males (see "Description" of respective species). As mentioned above, the ornamentation of the lower orbital margin is different between males and females. Also the ornamentation of the cheliped merus varies according to sex and different stages of development. We have found that the following characters are particularly useful in discriminating species: general shape of the carapace; development of the delineation of regions and ornamentation on the dorsal surface of the carapace; armature of the cheliped merus; length of the dactylus of the fourth pereopod; and the structure of the first gonopod. The shape of the ambulatory legs is also useful, although the ambulatory legs may become stouter with increase of the body size. In this study, the proportions of the merus and propodus of the fourth pereopod and of the propodus of the fifth pereopod are used as representatives.

***Ilyograpsus rhizophorae* Barnard, 1955**
(Figs. 2–5)

Ilyograpsus rhizophorae Barnard, 1955: 26, Fig. 8a–g; Kensley, 1981: 46 (list); Sawada et al., 2005: 862.
Ilyograpsus paludicola – Crosnier, 1965: 31, Figs. 36, 37, 38a, b, 39, 59; Fishelson, 1971: 128. Not *Ilyograpsus paludicola* (Rathbun, 1909).
Iliograpsus (sic) *paludicola* – Holthuis, 1977: 161.
Ilyograpsus vannini Sawada, Hosogi & Sakai, 2005: 853 (in part), Fig. 5B, D, F.

***Name bearing type.* –** Holotype: male (6.5 × 7.5 mm) (South African Museum, Cape Town, A10913), Inhambane, Mozambique, in mangrove swamps, coll. University of Cape Town, Jul.1954. Not available for study.

***Material examined.* – Ethiopia**: 3 males (CL 5.0–6.5 mm), 1 non-ovigerous female (CL 7.4 mm), paratypes of *Ilyograpsus vannini* (RMNH D 26501), Israel South Red Sea Expeditions 1962/2996, Melita Bay, Gulf of Zula, south of Massawa, mangrove swamps with *Avicennia marina* (Forskål), 0 to 0.5 m deep at low tide, 14 Apr.1962. **Madagascar**: 1 ovigerous female (CL 7.2 mm) (MNHN-B 12842), Tuléar, mangrove swamps, coll. A. Crosnier, 1 ovigerous female (CL 5.3 mm) (MNHN-B 12843); 1 non-ovigerous female (CL 4.4 mm), 2 ovigerous females (CL 5.2, 5.3 mm) (MNHN-B 12845), same locality, coll. Derijard; 1 male (CL 3.8 mm) (MNHN-B 12846), Nosy Bé, mangrove swamps, coll. A. Crosnier.

***Description of male.* –** Carapace (Figs. 3A, 4A) suboctogonal, breadth 1.21–1.33 times length (n = 4, mean 1.27); regions only faintly indicated in general, but gastrocardiac groove distinct. Postfrontal ridges low, straight, separated by broad median sulcus. Epigastric ridges absent. Lateral margins generally convex, greatest carapace breadth between external orbital teeth or third anterolateral teeth. Four anterolateral teeth present, first tooth (external orbital tooth) largest, subacute; second tooth extending as far as or slightly exceeding external orbital tooth, rounded or bluntly pointed; third tooth laterally extending as far as or clearly exceeding beyond external orbital tooth, varying from blunt to acuminate; fourth tooth tiny, but clearly demarcated, blunt or subacute; sometimes slight notch present posterior to fourth tooth. Mesobranchial region with some short striae. Front prominent, distinctly narrower than base of front, 0.30–0.35 times front-orbital width (n = 4) and wider than orbit; anterior margin faintly bilobed in dorsal view. Upper orbital margin sinuous, slightly oblique; lower orbital margin (Fig. 3B) with 2 or 3 lobules laterally.

Ocular peduncle (Fig. 3A) reaching external orbital tooth, length about 2.2–2.3 of corneal width; cornea slightly dilated.

Cheliped of large males (cl 6.3, 6.5 mm; RMNH D 26501) relatively large (Fig. 3E–G). Merus not markedly curved in dorsal view; posterior surface with granules sometimes forming short vertical rows; dorsal margin with small subdistal spine, inner surface with prominent short crest adjacent to inner-ventral margin; inner-distal angle with row of prominent granules. Carpus with inner angle weakly produced; dorsal margin delimited by row of granules; outer surface weakly granular; inner surface naked. Chela about 2.4 times as long as high; ventral margin faintly sinuous; outer surface of palm smooth; inner surface of palm with patch of dense setae extending onto fingers; fingers leaving proximal hiatus when closed; cutting edge of fixed finger with row of small, triangular teeth almost over entire length, distal part bordered by thin chitinous ridge; dactylus nearly straight, about 1.2 times longer than palm, cutting edge with well differentiated molar-like tooth medially and few obtuse teeth proximal to molar-like tooth and row of tiny teeth in distal 0.3, distal part bordered by chitinous ridge.

Cheliped of smallest male (cl 3.8 mm, MNHN-B 12846; Fig. 4B, C) with merus slightly curved, without patch of setae on anterior surface; dorsal margin with small subdistal spine; no short subdistal crest on anteroventral margin; posterior surface nearly smooth to slightly granular. Outer and dorsal surfaces of carpus nearly smooth or slightly granular; inner surface naked. Chela about 2.5 times as long as high; ventral margin slightly sinuous; outer surface of palm with scattered short setae; inner surface of palm with covering of numerous setae in distal half extending onto fingers; fingers leaving very narrow hiatus when closed, each with row of setae on outer and inner surfaces; cutting edge of fixed finger with row of small teeth; dactylus slightly curved, about 1.1 times longer than palm, cutting edge with row of small teeth, but without prominent tooth.

Ambulatory legs moderately long, slender (Fig. 2). Meri each with moderately large subdistal spine on anterior margin. Fourth pereopod (third ambulatory leg) (Fig. 3H) with merus 3.48–3.84 times longer than broad (n = 2), both anterior and posterior margins slightly convex; propodus 4.38–4.47 times longer than broad (n = 2); dactylus 0.74–0.80 (n = 2) times as long as propodus. Fifth pereopod (fourth ambulatory leg) (Fig. 3I) with propodus 2.81 times longer than broad (n = 1); dactylus slightly shorter than propodus.

Sixth pleonal somite (Fig. 3D) with slightly convex or nearly straight lateral margins, about 2.0–2.1 times broader than long. Telson rounded; breadth about 1.4–1.5 times length.

First gonopod (Fig. 3J–L) relatively slender, slightly sinuous

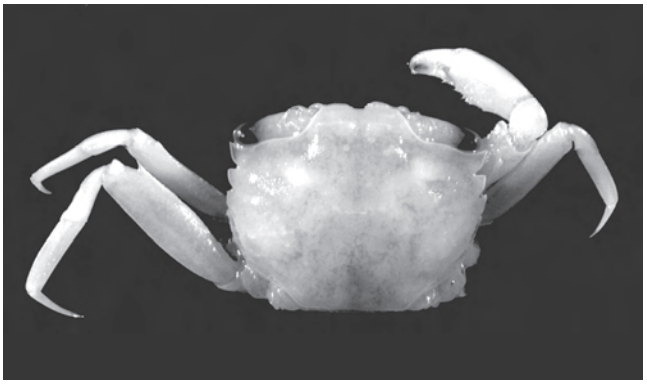

Fig. 2. *Ilyograpsus rhizophorae* Barnard, 1955. Male (cl 6.4 mm), paratype of *Ilyograpsus vannini* Sawada, Hosogi & Sakai, 2005, RMNH-D 26501, south of Massawa, Gulf of Zula, Ethiopia. Entire animal in dorsal view.

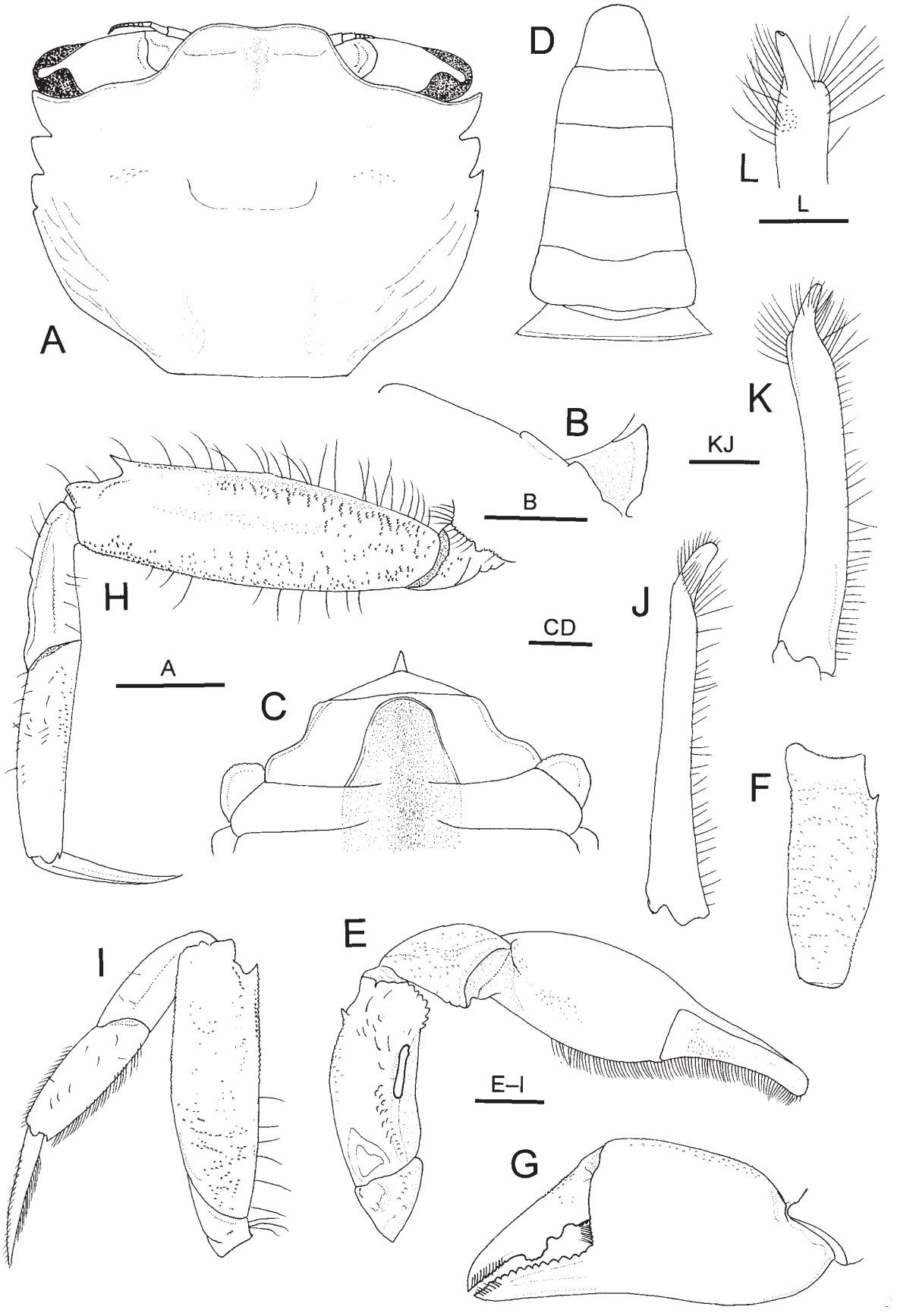

Fig. 3. *Ilyograpsus rhizophorae* Barnard, 1955. Male (cl 6.5 mm), paratype of *Ilyograpsus vannini* Sawada, Hosogi & Sakai, 2005, RMNH-D 26501, south of Massawa, Gulf of Zula, Ethiopia: A, carapace, ocular peduncles and antennae, dorsal view (setae omitted); B, left lower orbital margin and external orbital tooth, ventral view; C, anterior part of thoracic sternum, ventral view; D, pleon, ventral view; E, left cheliped, dorsal view; F, same, merus, outer view; G, same, chela, outer view; H, left fourth pereopod, dorsal view; I, left fifth pereopod, dorsal view; J, left first gonopod, ventral view; K, same, ventrolateral view; L, same, distal part, dorsal view. Scales: A = 2 mm; B–I = 1 mm; J–L = 0.5 mm.

in ventrolateral view; terminal process relatively long, slender, tube-like, weakly directed laterally, partially obscured by stiff setae; obtuse subterminal lobe delineated.

Description of female. – Carapace (Fig. 5A, B) generally similar to that of male; breadth 1.21–1.32 times length (n = 6, mean 1.26); greatest carapace breadth between third anterolateral teeth. Third anterolateral tooth exceeding beyond external orbital tooth or second anterolateral tooth. Lower orbital margin (Fig. 5C) bordered by row of 13–18 granules becoming larger and more widely spaced laterally.

Ocular peduncle (Fig. 5A) reaching external orbital tooth.

Cheliped (Fig. 5F–H) slender. Merus with small subdistal spine on dorsal margin. Carpus short. Chela about 3.8 times as long as high; outer surface faintly granular particularly dorsally and ventrally, dorsal margin slightly delimited by row of granules; inner surface of palm naked; fingers leaving very narrow hiatus when closed, with row of stiff setae on outer and inner surfaces in distal half; fixed finger slightly deflexed, cutting edge faintly dentate in proximal 0.6, remaining distal part bordered by thin chitinous ridge; dactylus slightly curved, cutting edge faintly denticulate in proximal 0.7, bordered by thin chitinous ridge in distal 0.3.

Fourth pereopod (third ambulatory leg) with merus 2.52 times longer than broad (n = 1); propodus 3.56 times longer than broad; dactylus 0.77 times as long as propodus. Fifth pereopod (fourth ambulatory leg) with propodus 3.59 times longer than broad; dactylus slightly shorter than propodus.

Size. – Males cl 3.8–6.5 mm; females cl 5.0–7.4 mm, ovigerous females cl 5.2–7.2 mm.

Distribution. – Western Indian Ocean: Ethiopia, Mozambique and Madagascar; mangrove swamps.

Remarks. – Barnard (1955) noted resemblance between his new taxon *Ilyograpsus rhizophorae* Barnard, 1955, and *Camptandrium paludicola* Rathbun, 1909, but he concluded that *I. rhizophorae* should belong to Grapsinae. Tesch (1918) had assigned *Camptandrium paludicola* to the Varuninae, Grapsidae. Later, Crosnier (1965) synonymized *I. rhizophorae* with *Camptandrium paludicola*, although the genus was maintained as valid. Recently, Sawada et al. (2005) reinstated *I. rhizophorae* as a valid species, but the authors' action was only based on a comparison of the original description of *I. rhizophorae* with the holotype (female) and one juvenile specimen of *I. paludicola*. They referred the specimens from Madagascar, identified with *I. paludicola* by Crosnier (1965), to their new taxon *I. vannini*, although they did not actually examine the specimens used by Crosnier (1965). Naruse & Kishino (2006) followed the action by Sawada et al. (2005) in recognizing *I. rhizophorae* as valid.

During this study, we tried to obtain information on the holotype of *I. rhizophorae* from the South African Museum. Unfortunately, because of the loan policy of the museum, direct examination of the holotype on loan was not possible. Although the original description and figures of Barnard (1955) is not fully detailed in the view point of the modern

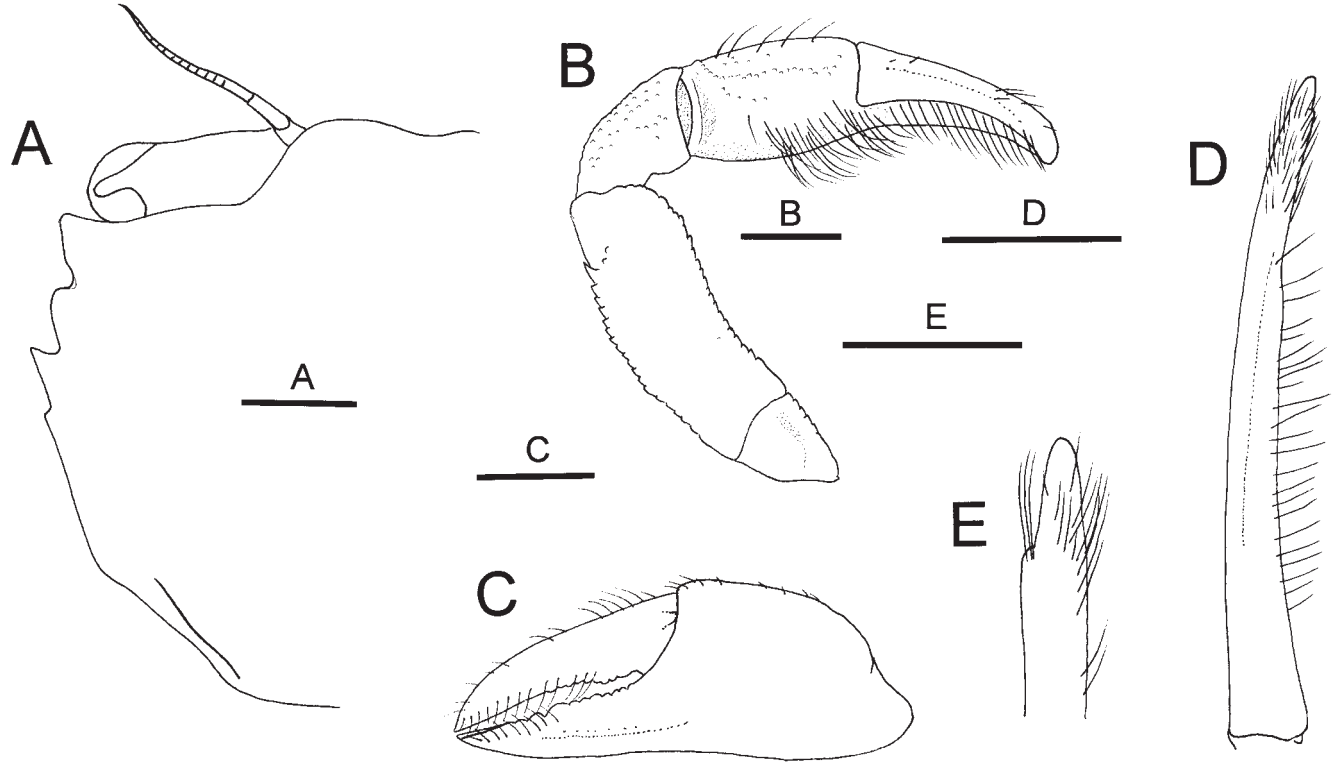

Fig. 4. *Ilyograpsus rhizophorae* Barnard, 1955. A, male (cl 5.0 mm), paratype of *Ilyograpsus vannini* Sawada, Hosogi & Sakai, 2005, RMNH-D 26501, south of Massawa, Gulf of Zula, Ethiopia; B–E, male (cl 3.8 mm), MNHN-B 12846, Nozy Bé, Madagascar. A, left part of carapace, left ocular peduncle and antenna, dorsal view; B, left cheliped, dorsal view; C, same, chela, outer view; D, right first gonopod, dorsal view; E, same, ventrolateral view. Scale bars: A, B, D = 1 mm; C, E = 0.5 mm.

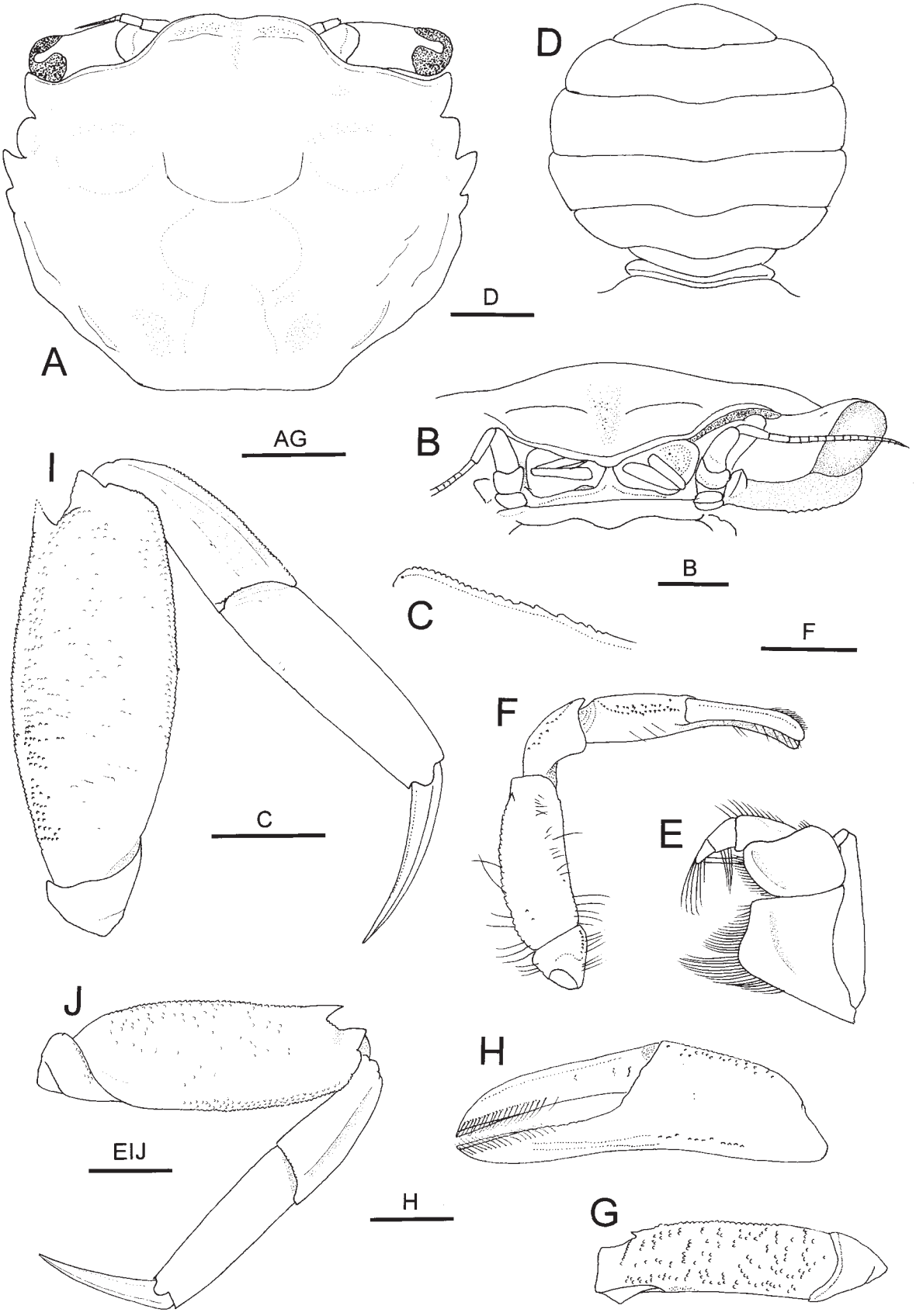

Fig. 5. *Ilyograpsus rhizophorae* Barnard, 1955. A–E, I, J, ovigerous female (cl 7.2 mm), MNHN-B 12842, Tuléar, Madagascar; F, H, ovigerous female (cl 5.3 mm), MNHN-B 12843, same locality; G, female (cl 7.4 mm), paratype of *Ilyograpsus vannini* Sawada, Hosogi & Sakai, 2005, RMNH-D 26501, south of Massawa, Gulf of Zula, Ethiopia. A, carapace, ocular peduncles and antennae, dorsal view; B, anterior part of cephalothorax, including left ocular peduncles and antennae, frontal view; C, left lower orbital margin, ventral view; D, pleon, ventral view; E, left third maxilliped, ventral view; F, left cheliped, dorsal view; G, same, merus, outer view; H, same, chela, outer view; I, right fourth pereopod, dorsal view; J, right fifth pereopod, dorsal view. Scale bars: A, D, F = 2 mm; B, C, E, G, I, J = 1 mm; H = 0.5 mm.

standard, some diagnostic characters are still apparent. These characters include the obscurely defined regions of the carapace, prominent anterolateral teeth of the carapace, and the elongate, relatively slender terminal lobe of the male first gonopod. The present specimens from Madagascar studied by Crosnier (1965) and the paratypes of *Ilyograpsus vannini* from Ethiopia agree rather well with the holotype of *I. rhizophorae* in these respects. Furthermore, all collecting localities, including the type locality of *I. rhizophorae*, are on the coasts of the western Indian Ocean. Therefore, we concluded to refer the present specimens from Madagascar and Ethiopia to *I. rhizophorae*.

Our comparison with the original description of *I. vannini* led us to conclude that *I. rhizophorae* and *I. vannini*, now represented only by the holotype, might be specifically distinct. Differences are seen in the shape of the carapace and the development of the anterolateral teeth on the carapace (Table 1). In the female specimens of *I. rhizophorae*, the carapace width is 1.21–1.32 of the carapace length, rather than 1.15 in *I. vannini*. The upper orbital margin appears more strongly oblique in *I. vannini* than in *I. rhizophorae*. The anterolateral teeth are more developed in *I. rhizophorae* than in *I. vannini*. The external orbital tooth reaches or slightly overreaches the distal margin of the cornea in the former specimens, but it does not reach the distal corneal margin in *I. vannini*. The second and third anterolateral teeth are more strongly developed in *I. rhizophorae* than *I. vannini*; the third anterolateral tooth clearly exceeds beyond the second tooth in the former specimens, rather than only extending as far as the second tooth in *I. vannini*.

Ilyograpsus rhizophorae is easily distinguished from other three congeneric species, *I. daviei* new species, *I. nodulosus* and *I. paludicola* by the poorly defined regions of the carapace and the relatively broader carapace (1.21–1.33 times wider than long vs. 1.05–1.21 times) (Table 1). The postfrontal ridges are less clearly demarcated in *I. rhizophorae* than in the other three species. There are no traces of epigastric ridges or tubercles in *I. rhizophorae*, whereas, in the latter three species, the carapace has at least traces of epigastric ridges or tubercles. The upper orbital margin is slightly oblique in *I. rhizophorae*, rather than transverse in the other three species. The terminal process of the first gonopod is well developed in *I. rhizophorae*, *I. paludicola* and *I. daviei*, new species, but the curvature of the process is different between *I. rhizophorae* and the other two species. In *I. rhizophorae*, the terminal process is curved laterally, whereas it is curved slightly dorsally in the latter two species.

Flores et al. (2003) described the first zoeal stage of *I. paludicola* from East African coast. During this study, however, the occurrence of *I. paludicola* in the western Indian Ocean has not been verified. It is highly likely that the authors were describing larvae of *I. rhizophorae*.

Ilyograpsus vannini Sawada, Hosogi & Sakai, 2005

Ilyograpsus paludicola — Vannini & Valmori, 1981: 77, Fig. 10C. Not *Ilyograpsus paludicola* (Rathbun, 1909)

Ilyograpsus vannini Sawada et al., 2005: 853 (in part), Figs. 1A–C, 3A, 5B, D, F.

Name bearing type.* –** Holotype: female (4.0 × 4.4 mm) (Museuo Zoologico, University of Florence 664), Abo, Somalia, coll. M. L. Azzaroli. Not available for study (see ***Remarks).

***Material examined.* –** None.

Remarks.* –** As discussed above, the paratypes of *Ilyograpsus vannini* from Melita Bay, Gulf of Zula, Ethiopia (RMNH D 26501), are here identified with *I. rhizophorae*. Unfortunately, the holotype and one paratype, both ovigerous females, from Abo, Somalia, were not available to us. We recognize the present taxon as a valid species for the time being, because of the differences seen in the shape of the carapace and the development of the anterolateral teeth on the carapace (see "Remarks***" of *I. rhizophorae*).

Sawada et al. (2005) cited Karachi, Pakistan, in the distribution of *I. vannini*, although they did not give any evidence.

Ilyograpsus nodulosus Sakai, 1983
(Figs. 6–8)

Iliograpsus [sic] *nodulosus* Sakai, 1983: 19, 42, Pl. 4, Fig. E.

Ilyograpsus nodulosus Kishino et al., 2001a: 16, Pl. 1(4); 2001b: 126; Nakasone & Irei, 2003: 273; Sawada et al., 2005: 857 (in part), Figs. 2A, D, 3B; Naruse, 2005: 221; Naruse & Kishino, 2006: 73, Figs. 2b, 5.

Ilyograpsus paludicola Yamaguchi et al., 1976: 41, Fig. 2(8); Fukuda, 1978: 15; Yamaguchi et al., 1987: 31, Pl. 14, Fig. 8; Nakasone & Irei, 2003: 273. Not *Ilyograpsus paludicola* (Rathbun, 1909).

Not *Ilyograpsus nodulosus* Sawada et al., 2005, Figs. 4C, 5A, C, E. = *Ilyograpsus paludicola* (Rathbun, 1909).

Name bearing type.* –** Holotype: sex not indicated (cl 3.9, cw 4.2 mm), mangroves of Kuira River, Iriomote Island, Yaeyama Islands, coll. H. Yoshikawa. Presumably no longer extant (Naruse & Kishino, 2006; pers. obs.). See ***Remarks.

***Material examined.* – Japan**. 1 ovigerous female (cl 5.7 mm), CBM-ZC 9418, Waka River estuary, 14 Jul.1999, coll. A. Nomoto; 1 male (cl 4.0 mm), CBM-ZC 9419, Kinokawa River estuary, Wakayama, Wakayama Prefecture, 15 Jul.1999, coll. A. Nomoto; 1 male (cl 4.4 mm), CBM-ZC 9420, Funao, Kainan, Wakayama Prefecture, 13 Jul.1999, coll. A. Nomoto; 5 males (cl 3.3–4.5 mm), 1 female (cl 4.6 mm), 3 ovigerous females (cl 5.7–7.5 mm), CBM-ZC 9304, Arita River estuary at Koemi, Arita, Wakayama Prefecture, 5 May 2004, mud, dip net, coll. A. Nomoto; 1 ovigerous female (cl 5.6 mm), CBM-ZC 9421, Hidaka River estuary, Shioya, Gobo, Wakayama Prefecture, 30 Jul.2000, coll. A. Nomoto; 2 males (cl 3.1, 3.6 mm), CBM-ZC 9422; Fukuro, Shirahama, Wakayama Prefecture, 19 Aug.2001, coll. T. Watanabe; 1 female (cl 3.8 mm), CBM-ZC 9305, Mukai-higashi-cho, Onomichi, Hiroshima Prefecture, Seto Inland Sea, tidal flat, mud, 8 Aug.2002, dip net, coll. A. Nomoto; 3 male (cl 2.8–3.6 mm), 1 female (cl 3.9 mm), CBM-ZC 9306, Mishou Bay, Minami-Uwa District, Ehime Prefecture, subtidal, 19 Apr.2004, coll.

Table 1. Comparison among five species of *Ilyograpsus* Barnard, 1955. *Data after Sawada et al. (2005). For proportions, mean values are given in parentheses.G1: first gonopod.

	I. rhizophorae	*I. vannini**	*I. nodulosus*	*I. paludicola*	*I. daviei, new species*
Carapace					
Width/length (♂/♀)	1.21–1.33 (n=4, 1.27)/ 1.21–1.32 (n=6, 1.26)	1.15 (only female)	1.06–1.14 (n=19, 1.10)/ 1.05–1.19 (n=25, 1.12)	1.08–1.17 (n=10, 1.13)/ 1.09–1.19 (n=12, 1.13)	1.12–1.19 (n=6, 1.15)/ 1.15–1.21 (n=11, 1.19)
Regions	poorly defined	poorly defined	strongly defined	well defined	relatively weakly defined
Postfrontal ridges	less distinct	less distinct	distinct, often crested	distinct, often crested	distinct
Epigastric ridges	absent	absent	present	present	present or rudimentary
Second anterolateral tooth	moderately large	small	moderately large	moderately large	moderately large
Third anterolateral tooth in females	well exceeding beyond second tooth	exceeding nearly as far as second tooth	well exceeding beyond second tooth	well exceeding beyond second tooth	well exceeding beyond second tooth
Upper orbital margin	slightly oblique	oblique	transverse	transverse	transverse
Lower orbital margin (♂/♀)	with distinct lobules/ with row of 13–18 small, unequal granules	unknown	without distinct lobules/ with row of 20–23 minute granules	with distinct lobules/ with row of 13–18 small, unequal granules	with distinct lobules/ with row of 13–18 small, unequal granules
Merus of cheliped	with subdistal spine	with subdistal spine	unarmed or with minute tubercles subdistally	with subdistal spine	with subdistal spine
Fourth pereopod					
Merus length/width (♂/♀)	3.48–3.84 (n=2, 3.66)/ 2.52 (n=1)	unavailable	3.40–4.64 (n=10, 4.14)/ 2.72–4.00 (n=13, 3.52)	3.21–4.12 (n=8, 3.69)/ 3.17–3.79 (n=7, 3.50)	2.47–3.02 (n=5, 2.88)/ 2.24–2.77 (n=10, 2.56)
Propodus length/width (♂/♀)	4.38–4.47 (n=2, 4.43)/ 3.56 (n=1)	unavailable	4.07–5.80 (n=11, 5.00)/ 4.08–5.38 (n=12, 4.66)	4.16–5.90 (n=8, 5.14)/ 4.69–6.00 (n=6, 5.08)	3.27–3.58 (n=5, 3.44)/ 3.18–3.85 (n=10, 3.41)
Dactylus/propodus (♂/♀)	0.74–0.80 (n=1, 0.77)/ 0.77 (n=1)	unavailable	0.87–1.02 (n=11, 0.95)/ 0.90–1.04 (n=11, 0.97)	0.68–0.80 (n=8, 0.77)/ 0.71–0.89 (n=7, 0.82)	0.64–0.87 (n=5, 0.80)/ 0.72–0.86 (n=10, 0.80)
Fifth pereopod					
Propodus length/width (♂/♀)	2.81 (n=1)/3.59 (n=1)	unavailable	2.55–3.33 (n=11, 3.03)/ 2.63–3.36 (n=11, 2.93)	3.03–4.27 (n=9, 3.61)/ 2.83–3.27 (n=7, 3.27)	2.00–2.87 (n=5, 2.43)/ 2.05–2.45 (n=9, 2.09)
Terminal process of G1	moderately long, curved laterally	unknown	short, subtruncate	moderately long, slightly curved dorsally	moderately long, slightly curved dorsally

K. Wada; 1 female (cl 3.7 mm), 1 ovigerous female (cl 5.1 mm), CBM-ZC, similar locality, 20 Apr.2004, coll. K. Wada; 1 ovigerous female (cl 6.5 mm), SINH-CR 1151, Kaminokae River, Nakatosa-cho, 16 Jun.2004, coll. A. Yamamoto; 1 ovigerous female (cl 5.6 mm), SINH-CR 1152, same data as SINH-CR 1151; 1 ovigerous female (cl 6.0 mm), SINH-CR 1257, Nishi-nada, Urado Bay, Kochi, Kochi Prefecture, 21 Jun.2004, coll. A. Yamamoto; 1 male (cl 4.1 mm), SINH-CR 1258, same data as SINH-CR 1257; 1 male (cl 4.2 mm), SINH-CR 1259, same data as SINH-CR 1257; 1 ovigerous female (cl 5.7 mm), SINH-CR 1274, Nishi-nada, Urado Bay, 22 Jun.2004, coll. A. Yamamoto; 4 ovigerous females (cl 4.7–6.9 mm), SINH-CR 1275, same data as SINH-CR 1274; 2 ovigerous females (cl 5.3, 6.1 mm), SINH-CR 1350, Suzaki, Kochi Prefecture, 9 Apr.2004, coll. A. Yamamoto; 1 ovigerous female (cl 6.0 mm), SINH-CR 1371, Suzaki, 4 Jul.2004, coll. A. Yamamoto; 1 male (cl 4.0 mm), SINH-CR 1372, same data as SINH-CR 1371; 17 males (cl 5.6 mm), 30 females (cl 4.8–6.6 mm), SINH-CR 1373, same data as SINH-CR 1371; 1 male (cl 3.2 mm), 4 ovigerous females (cl 4.5–5.5 mm), SINH-CR 1418, Fukaura, Urado Bay, 7 Jun.2004, coll. A. Yamamoto; 1 ovigerous female (cl 7.8 mm), SINH 1474, Nada, Urado Bay, 3 Aug.2004, coll. A. Yamamoto; 2 ovigerous females (cl 5.6, 5.7 mm), SINH-CR 1493, Suzaki, 5 Aug.2004, coll. A. Yamamoto; 1 male (cl 3.1 mm), 2 ovigerous females (cl 4.9, 6.3 mm), SINH-CR 1522, Sakura-gawa rivermouth estuary, Suzaki, Kochi Prefecture, 20 Apr.2004, coll. A. Yamamoto; 2 males (cl 3.8, 4.1 mm), CBM-ZC 9386, Shimanto River estuary at Shimoda, Nakamura, Kochi Prefecture, tidal flat, mud, dip net, 4 Jun.2004, coll. A. Nomoto; 3 males (cl 3.2–4.1 mm), 3 females (cl 3.4–5.4 mm), CBM-ZC 9387, Tomouchi River estuary, Nobeoka, Miyazaki Prefecture, 27 Apr.2006, beach seine, coll. N. Sakai; 3 males (cl 2.7–4.5 mm), 2 ovigerous females (cl 4.4, 4.9 mm), CBM-ZC 9233, Yanma, Sumiyo Village, Amami-Oshima Island, 31 Mar.2002, coll. T. Kishino; 2 ovigerous females (cl 6.4, 6.5 mm), CBM-ZC 9232, Naikai, Sumiyo Village, Amami-Oshima Island, 2 May.2003, coll. T. Kishino; 2 ovigerous females (cl 4.8, 4.9 mm), CBM-ZC 8841, Yanma Port, mudflat, under rock, Sumiyo Village, Amami-Oshima Island, intertidal, 28 Apr.2006, hand, coll. T. Komai; 1 female (cl 4.3 mm), 1 ovigerous female (cl 4.9 mm), CBM-ZC 9224, Fukuchi River estuary, Ginoza Village, Okinawa Island, 5 Aug.2001, coll. T. Kishino; 1 ovigerous female (cl 6.1 mm), RUMF-ZC-242, Tima River estuary, Nago, Okinawa Island, 24 Apr.2005, coll. T. Naruse; 2 females (cl 4.0, 4.1 mm), ZRC 2005.0114, Tima River estuary, Nago, Okinawa Island, 13 Feb.2005, coll. T. Naruse; 2 males (cl 3.5, 3.6 mm), 1 ovigerous female (cl 5.5 mm), CBM-ZC 9235, Shiira River estuary, Iriomote Island, Yaeyama Islands, 22 Mar.2005, coll. T. Naruse; 3 males (cl 3.3–3.4 mm), 1 female (cl 4.9 mm), Shirahama, Iriomote Island, sea grass beds on tidal flat, 23 Jun.2005, dip net, coll. T. Komai.

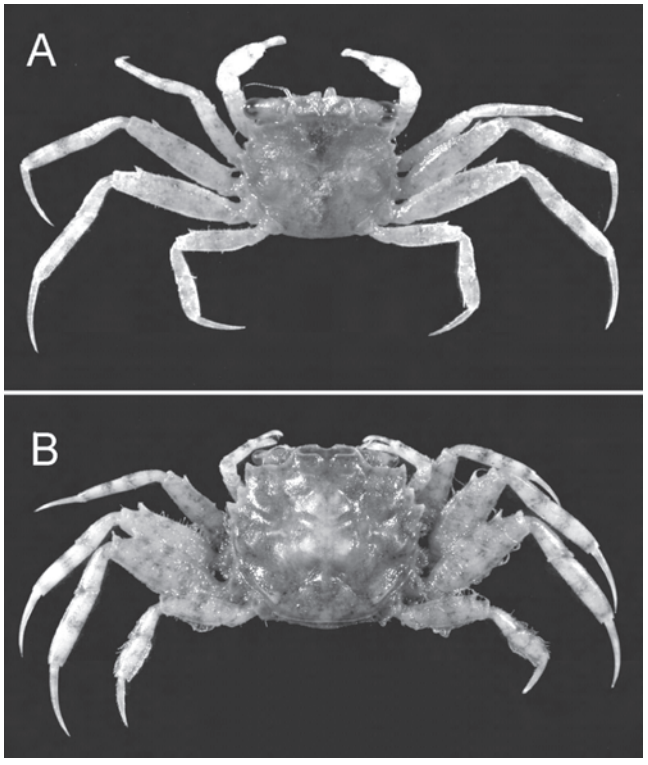

Fig. 6. *Ilyograpsus nodulosus* Sakai, 1983. Entire animals in dorsal view. A, male (cl 4.3 mm), SINH-Cr 1373, Suzaki, Kochi Prefecture, Japan; B, ovigerous female (cl 7.8 mm), SINH-Cr 1474, Nada, Urado Bay, Kochi, Kochi Prefecture, Japan.

***Description of male.* –** Carapace (Fig. 7A, B) suboctogonal, breadth 1.06–1.14 times length (n = 19, mean 1.10); regions clearly defined. Postfrontal ridges distinct, often crested. Epigastric ridges or tubercles present. Cardiac region with paired low elevations; branchial regions with 2 pairs of low elevations on either side of gastro-cardiac region, and with 2 short longitudinal ridges laterally. Lateral margins generally convex, greatest carapace breadth between third anterolateral teeth. Four anterolateral teeth present, first tooth (external orbital tooth) largest, subacute or acute; second tooth extending as far as or slightly exceeding external orbital tooth, rounded or bluntly triangular; third tooth extending clearly exceeding beyond external orbital tooth, varying from blunt to acuminate; fourth tooth small, but clearly delineated, blunt or subacute; sometimes slight notch posterior to fourth tooth. Front prominent, distinctly bilobed, less than hind width, about 0.4 times front-orbital width, wider than orbit. Upper orbital margin slightly sinuous, nearly transverse; lower orbital margin granular, without conspicuous lobules laterally.

Ocular peduncle (Fig. 7A, B) overreaching external orbital tooth, length about 2.2–2.3 of corneal width; cornea not dilated.

Cheliped (Fig. 7E–G) relatively small. Merus with or without minute subdistal granule on dorsal margin; no distinct subdistal crest on anteroventral margin. Chela about 2.7 times as long as high; cutting edge of fixed finger with row of small blunt teeth in proximal 0.8 and thin chitinous ridge in distal 0.2; dactylus slightly curved, about 1.2–1.3 times longer than palm, cutting edge with row of small rounded teeth in proximal 0.7, remainder bordered by thin chitinous ridge.

Ambulatory legs (Fig. 6A) relatively long, slender. Meri each with relatively large subdistal spine. Fourth pereopod (third ambulatory leg) (Fig. 7H) with merus 3.40–4.64 times longer than broad (n = 10, mean 4.14), anterior margin faintly sinuous or straight, posterior margins slightly convex; propodus 4.07–5.80 times longer than broad (n = 10, mean 5.00); dactylus 0.87–1.02 times as long as propodus (n = 11, mean 0.95). Fifth pereopod (fourth ambulatory leg) (Fig. 7I) with propodus 2.55–3.33 times longer than broad (n = 11, mean 3.03), outer and inner margins fringed with short setae; dactylus longer than propodus.

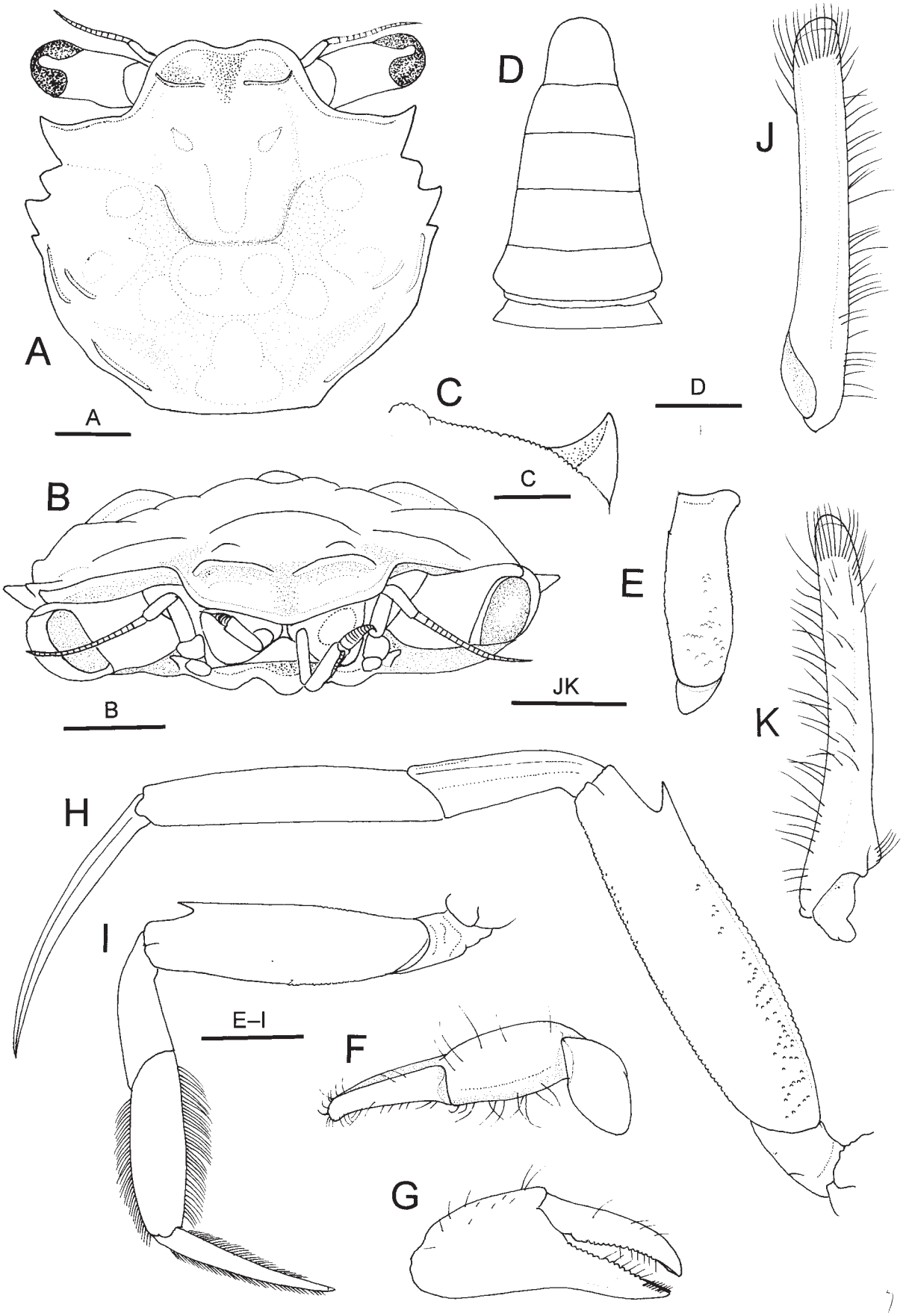

Fig. 7. *Ilyograpsus nodulosus* Sakai, 1983. Male (cl 4.9 mm), SINH-Cr 1373, Suzaki, Kochi Prefecture, Japan. A, carapace, ocular peduncles and antennae, dorsal view; B, cephalothorax and cephalic appendages, frontal view; C, left lower orbital margin and external orbital tooth, ventral view; D, pleon, ventral view; E, merus of right cheliped, outer view; F, chela and carpus of right cheliped, dorsal view; G, right chela, outer view; H, left fourth pereopod, dorsal view; I, left fifth pereopod, dorsal view; J, left first gonopod, ventral view; K, same, dorsal view. Scale bars: A, B, D, E–I = 1 mm; C, J, K = 0.5 mm.

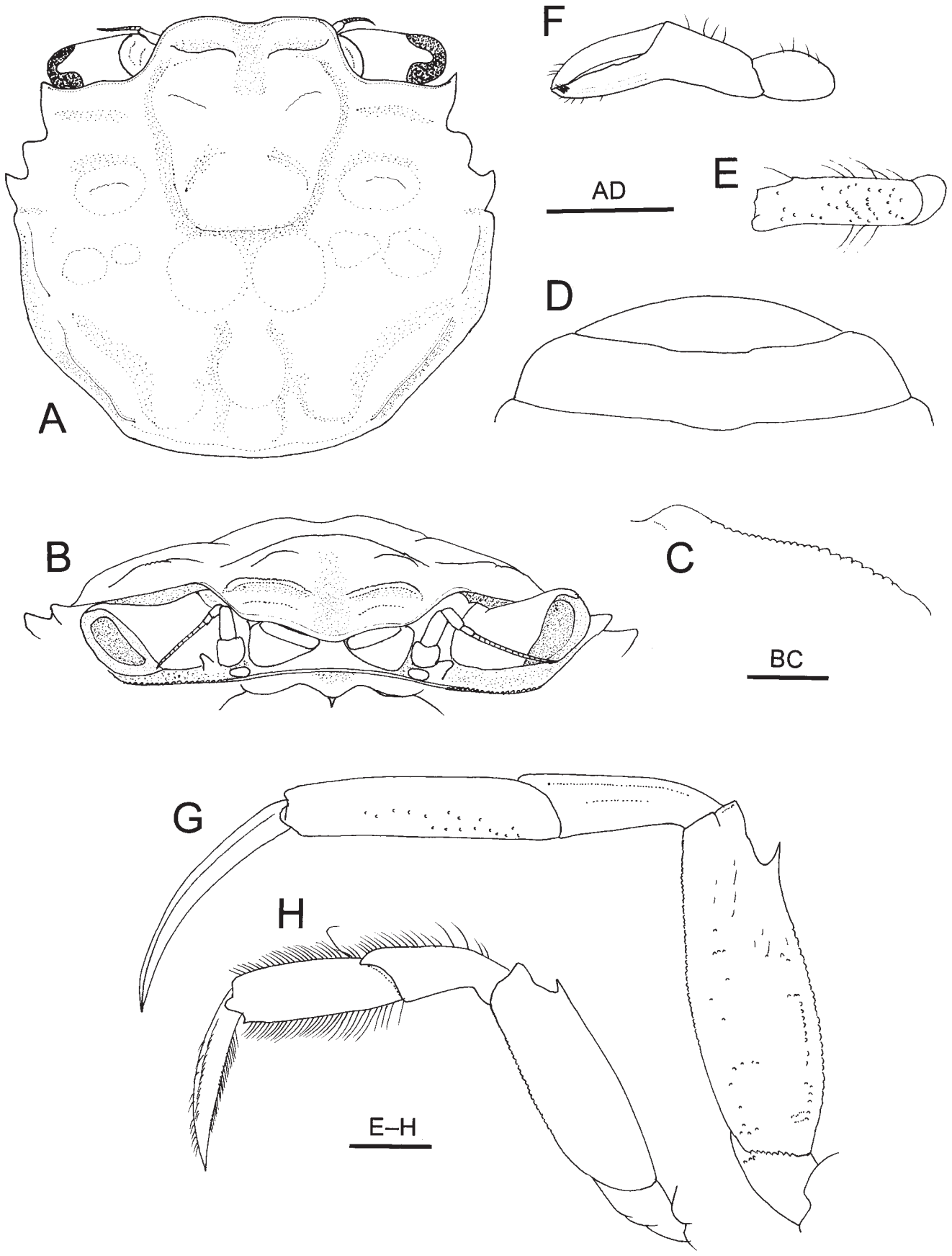

Fig. 8. *Ilyograpsus nodulosus* Sakai, 1983. Female (cl 7.8 mm), SINH-Cr 1474, Nada, Urado Bay, Kochi, Kochi Prefecture, Japan. A, carapace, ocular peduncles and antennae, dorsal view (setae omitted); B, cephalothorax and cephalic appendages, frontal view; C, left lower orbital margin, ventral view; D, sixth pleonal somite and telson, ventral view (setae omitted); E, merus of left cheliped, outer view; F, carpus and chela of left cheliped, outer view; G, left fourth pereopod, dorsal view; H, left fifth pereopod, dorsal view. Scale bars: A, D = 2 mm; B, E–H = 1 mm; C = 0.5 mm.

Sixth pleonal somite (Fig. 7D) with slightly convex lateral margins, about 2.6–2.7 times broader than long. Telson rounded terminally; breadth about 1.1–1.2 times length.

First gonopod (Fig. 7J, K) relatively stout, very slightly curved; terminal process very short, truncate, partially obscured by stiff setae.

***Description of female.* –** Carapace (Fig. 8A, B) breadth about 1.05–1.19 (n = 25, mean 1.12) times length; greatest carapace breadth between third anterolateral teeth. Regions on dorsal surface well defined; elevations on dorsal surface sometimes ornamented by short granular ridges or tubercles; cardiac region divided in 3 lobes (2 anterior and 1 posterior). Second anterolateral tooth exceeding external orbital tooth. Third anterolateral tooth distinctly exceeding second anterolateral tooth. Lower orbital margin (Fig. 8C) bordered by row of 20–23 minute granules.

Ocular peduncle (Fig. 8A) reaching external orbital tooth.

Cheliped (Fig. 8E, F) generally similar to that of *I. rhizophorae*. Dorsal margin of merus with minute denticle or tubercle subdistally or completely unarmed. Chela about 3.4 times as long as high; ventral margin concave with fixed finger weakly deflexed; cutting edge of fixed finger faintly denticulate in proximal 0.8 and bordered by thin chitinous ridge in distal 0.2; dactylus slightly curved, cutting edge nearly smooth in proximal 0.7, bordered by thin chitinous ridge in distal 0.2.

Ambulatory legs (Fig. 6B) relatively longer, more slender compared with congeners. Meri each with relatively large subdistal spine on anterior margin. Fourth pereopod (third ambulatory leg) with merus 2.72–4.00 times longer than broad (n = 13, mean 3.52), anterior margin sinuous; propodus 4.08–5.38 times longer than broad (n = 12, mean 4.66); dactylus 0.90–1.04 times as long as propodus (n = 11, mean 0.97). Fifth pereopod (fourth ambulatory leg) with propodus 2.63–3.36 times longer than broad (n = 11, mean 2.93), outer and inner margins with fringe of short stiff setae; dactylus subequal to or longer than propodus.

***Size.* –** Males cl 2.8–4.5 mm; females cl 3.9–7.8 mm, ovigerous females cl 4.4–7.8 mm.

***Colour in life.* –** Entirely muddy brown; ambulatory legs with faint darker bands.

***Distribution.* –** Known with certainty only from southern Japan, including Seto Inland Sea, Shikoku, Kyushu and Ryukyu Islands southward to Iriomote Island in Yaeyama Islands.

***Remarks.* –** As Naruse & Kishino (2006) noted, the holotype of *Ilyograpsus nodulosus* has not been located, and it is highly possible that it has been lost after the death of Prof. T. Sakai. However, the present material contains topotypic specimens from the Iriomote Island, and there is no serious problem in establishing the taxonomic identity of the taxon. The available material suggests that male attains much smaller size than female does in this species.

As noted before, *Ilyograpsus nodulosus* appears closest to *I. paludicola*. Shared characters include: the regions of the carapace are relatively well defined, particularly in males; epigastric ridges or tubercles are present on the carapace; the ambulatory legs are relatively long and slender. *Ilyograpsus nodulosus* is distinguished from *I. paludicola* by the following characters (Table 1). The lower orbital margin in females bears 20–23 minute granules in *I. nodulosus*, rather than 13–18 small, unequal granules in *I. paludicola*. The merus of the cheliped lacks a distinct subdistal spine on the dorsal margin and a short subdistal crest on the anteroventral margin in *I. nodulosus*, whereas these structures are well developed in *I. paludicola*. The ambulatory legs are more slender in *I. nodulosus* than in *I. paludicola*, though sexual difference should be concerned. The dactylus of the fourth pereopod is proportionally longer in *I. nodulosus* than in *I. paludicola*. The terminal margin of the first gonopod of *I. nodulosus* is truncate with a poorly developed terminal process. In. *I. paludicola*, the terminal process of the first gonopod is conspicuous.

We have examined material from various localities in the Indo-West Pacific, but the occurrence of *I. nodulosus* outside of the Japanese Archipelago was not confirmed. On the other hand, the occurrence of *I. paludicola* in Japan was not confirmed too. Thus, we consider that previous records of *I. paludicola* (see Yamaguchi et al., 1976, 1987; Fukuda, 1978; Nakasone & Irei, 2003) were results of misidentifications, and they are all referred to *I. nodulosus*. Sawada et al. (2005) identified a single ovigerous female from Nouméa, New Caledonia and nine specimens from Brisbane River, Brisbane, Queensland, Australia, with *I. nodulosus*, but later Naruse & Kishino (2006) questioned the identification. After reexamination, we have confirmed that the specimen from New Caledonia (ovigerous female, OMNH-Ar 1656) actually represents *I. paludicola* (see ***Remarks*** of *I. paludicola*). Specimens from Queensland we have examined during this study all represent *I. daviei*, new species, and thus there is little doubt that the specimens from the Brisbane River used by Sawada et al. (2005) could represent *I. daviei*, new species.

Ilyograpsus paludicola (Rathbun, 1909)

(Figs. 9–12)

Camptandrium paludicola Rathbun, 1909: 109; 1910: 326, Fig. 9a, b; Tesch, 1918: 68; Shen, 1935: 31.

Ilyograpsus paludicola — Takeda & Nunomura, 1976: 84; Tirmizi et al., 1985: 24, Fig. 1; Tirmizi & Ghani, 1996: 143, Fig. 55; Davie, 2002: 229 (in part); Yeo et al., 2004: Sawada et al., 2005: 861 (in part), Figs. 2B, C, 4A, B; Naruse & Kishino, 2006: 75.

Ilyograpsus nodulosus — Sawada et al., 2005: 857 (in part), Fig. 4C.

Not *Ilyograpsus paludicola* — Crosnier, 1965: 31, Figs. 36–37, 38a, b, 39, 59; Fishelson, 1971: 128; Kensley, 1981: 46 (list). = *Ilyograpsus rhizophorae* Barnard, 1955.

Not *Ilyograpsus paludicola* — Hartnoll, 1975: 307 (table I), 311 (table II). = ?*Ilyograpsus rhizophorae* Barnard, 1955.

Not *Iliograpsus* (sic) *paludicola* — Holthuis, 1977: 161. = *Ilyograpsus rhizophorae* Barnard, 1955].

Not *Ilyograpsus paludicola* — Yamaguchi et al., 1976: 41, Fig. 2(8); Nakasone, 1977: 62; Fukuda, 1978: 15; Yamaguchi et al., 1987: 31, Pl. 14, Fig. 8; Nakasone & Irei, 2003: 273. = *Ilyograpsus nodulosus* Sakai, 1983.

Not *Ilyograpsus paludicola* — Vannini and Valmori, 1981: 77, Fig. 10C. = *Ilyograpsus vannini* Sawada, Hosogi & Sakai, 2005.

***Name bearing type.* –** Holotype: female (4.5 × 5.3 mm), Zoological Museum, University of Copenhagen (ZMUC) reg. no. 7692, Lem Ngob, Gulf of Thailand, 23–27 Dec.1899, coll. Th. Mortensen. Not examined.

***Material examined*. – Vietnam:** 1 male (cl 10.4 mm), CBM-ZC 9307, Giao Thuy, Nam Dinh, 17 May 2001, coll. Do Van Nhuong. **Indonesia**: 1 male (cl 3.1 mm), 1 ovigerous female (cl 4.2 mm), CBM-ZC 9423, Benoa Bay, Bali, 31 Aug.2001, coll. K. Wada; 1 ovigerous female (cl 5.7 mm), ZRC 1965.7.9.17, Padang, Sumatra, 1963, coll. R. Serène; 4 males (cl 2.8–4.2 mm), 3 females (cl 2.8–4.9 mm), 3 ovigerous females (cl 4.0–8.0 mm), 1 juvenile (cl 2.5 mm), ZRC 1998.10.30, Bintan, Jun.1995, coll. P. K. L. Ng & L. G. S. Tan. **Malaysia**: 1 male (cl 3.7 mm), ZRC 1965.10.8.3, Trengganu, Kuala Ibai, Aug.1950, coll. M. W. F. Tweedie; 1 female (cl 4.4 mm), ZRC 1965.10.8.6, Labuan, 1938; 1 female (cl 4.6 mm), ZRC 1965.10.8.7, Prai, Province Wellesley, 1938. **Singapore**: 1 ovigerous female (cl 4.1 mm), ZRC 1965.10.8.5, Jurong River, 18 Aug.1934. **Australia**: 1 male (cl 4.5 mm), QM W 19155, Camerons Beach, Northern Territory, 12°21'S 130°59.6'E, mangroves, soft mud flat, 30 Jun.1996, coll. P. Davie; 1 female (cl 4.6 mm), QM W 25018, Reichard Creek, Darwin Harbor, Northern Territory, 12°27'S 130°50'E, estuarine, littoral, open *Rhizophora* forest, Nov.1998, coll. C. Salgado; 4 males (cl 4.6–7.4 mm), QM W 29749, Darwin Harbor, Northern Territory, 2004, coll. K. Metcalfe. **New Caledonia**: 1 ovigerous female (cl 8.5 mm), OMNH-Ar 1656, near Nouméa, 14 Oct.1958.

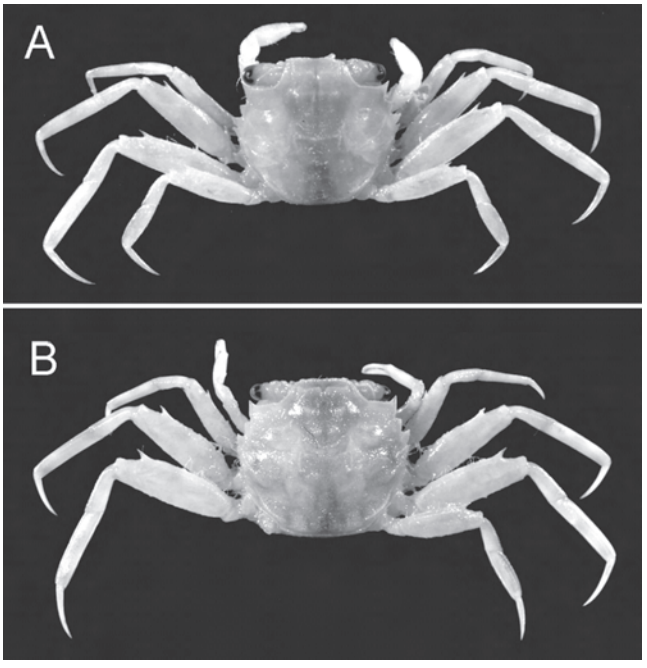

Fig. 9. *Ilyograpsus paludicola* (Rathbun, 1909). Entire animals in dorsal view. A, male (cl 4.3 mm), ZRC 1998-1030, Bintan, Indonesia; B, female (cl 8.0 mm), same lot.

***Description of male.* –** Carapace (Figs. 10A, B, 11A) suboctogonal, breadth 1.08–1.17 times length (n = 10, mean 1.13); regions well defined (degree still less than in *I. nodulosus*). Postfrontal ridges distinct, often crested, separated by broad median sulcus. Epigastric ridges or tubercles present. Cardiac region with paired low elevations; branchial regions with 1 or 2 pairs of low elevations on either side of gastro-cardiac region, and few short longitudinal ridges laterally. Lateral margins generally convex, greatest carapace breadth between third anterolateral teeth. Four or five anterolateral teeth present, first tooth (external orbital tooth) largest, triangular, acute or subacute; second tooth extending as far as or slightly exceeding external orbital tooth, rounded or bluntly triangular; third tooth clearly exceeding beyond external orbital tooth, varying from blunt to acute; fourth tooth small, but clearly delineated, blunt or subacute; fifth tooth, if present, very small. prominent, distinctly less than posterior width, about 0.40 times front-orbital width and wider than orbit; anterior edge in dorsal view faintly bilobed. Upper orbital margin concave or slightly sinuous, almost transverse; lower orbital margin (Figs. 10C, 11B) with 2–4 lobules laterally.

Ocular peduncle (Figs. 10A, B; 11A, B) reaching or slightly overreaching external orbital tooth, length about 2.2–2.3 of corneal width; cornea not dilated.

Cheliped of largest specimen (cl 10.4 mm, CBM-ZC 9307; Fig. 11C–E) with relatively strong subdistal spine on dorsal margin of merus; inner margin of merus with or without prominent short crest; inner distal angle of merus with row of small granules. Chela 2.4 times as long as high; ventral margin faintly sinuous; outer surface of palm smooth; inner surface of palm with patch of dense setae extending onto fingers; fingers leaving proximal hiatus when closed; cutting edge of fixed finger with row of small, triangular teeth almost over entire length, distal part bordered by thin chitinous ridge; dactylus nearly straight, shorter than palm, cutting edge with well differentiated molarlike tooth proximal to midlength, otherwise weakly dentate, distal part bordered by chitinous ridge.

Cheliped of other specimens (Fig. 10E–G) proportionally smaller, each with distinct subdistal spine on dorsal margin of merus; anteroventral margin with or without short, smooth crest subdistally (Fig. 10F). Carpus with inner angle weakly produced. Chela about 2.4 times longer than high; outer surface with scattered short setae. Cutting edge of fixed finger with row of small rounded teeth in proximal 0.7 and thin chitinous ridge in distal half; dactylus slightly curved, 1.1 times longer than palm, cutting edge with row of small rounded teeth in proximal half, nearly smooth in distal half.

Ambulatory legs (Fig. 9A) relatively long, slender. Meri each with relatively large subdistal spine. Fourth pereopod (third ambulatory leg) (Figs. 10I; 11F) with merus 3.21–4.12 times longer than broad (n = 8, mean 3.69); propodus 4.16–5.90 times longer than broad (n = 8, mean 5.14), anterior margin slightly sinuous, posterior margins slightly convex or nearly

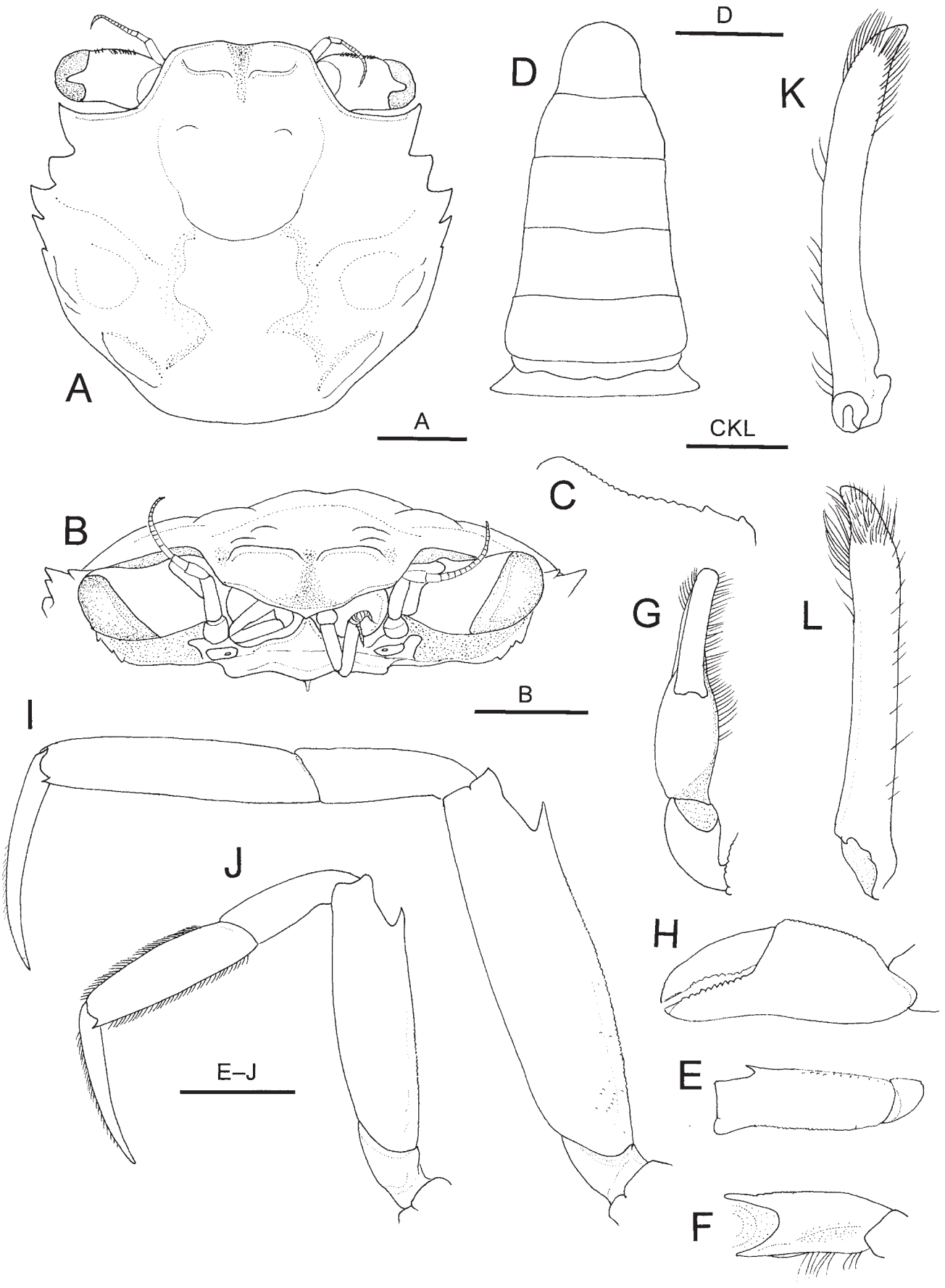

Fig. 10. *Ilyograpsus paludicola* (Rathbun, 1909). Male (cl 4.3 mm), ZRC 1998-1030, Bintan, Indonesia. A, carapace, ocular peduncles and antennae, dorsal view; B, cephalothorax and cephalic appendages, frontal view; C, lower orbital margin, ventral view; D, pleon, ventral view; E, merus of left cheliped, outer view; F, same, ventral view; G, carpus and chela of left cheliped, dorsal view; H, left chela, outer view; I, left fourth pereopod, dorsal view (setae omitted); J, fifth pereopod, dorsal view (setae partially omitted); K, left first gonopod, ventrolateral view; L, same, dorsal view. Scale bars: A, B, D, E–J = 1 mm; C, K, L = 0.5 mm.

straight; dactylus 0.68–0.80 times as long as propodus (n = 8, mean 0.77). Fifth pereopod (fourth ambulatory leg) (Figs. 10J; 11G) with propodus 3.03–4.27 times longer than broad (n = 9, mean 3.61), outer and inner margins fringed with short setae; dactylus shorter than propodus.

Sixth pleonal somite (Fig. 10D) with slightly convex lateral margins, about 2.6–2.7 times broader than long. Telson rounded terminally; breadth about 1.1–1.2 times length.

First gonopod (Figs. 10K, L; 11H) slender, slightly curved mesially; terminal process (Fig. 11I) relatively long, slightly curved dorsally, obscured by numerous stiff setae; subterminal lobe present in largest specimen.

***Description of female.* –** Carapace (Fig. 12A, B) generally similar to that of male, but with low, sometimes distinct short ridges or tubercles on gastric (1 or 2 pairs), cardiac (1 pair) and branchial (2 or 3 pairs) regions; breadth 1.09–1.19 times length (n = 12, mean 1.13); greatest carapace breadth between third anterolateral teeth. Third anterolateral tooth exceeding beyond external orbital tooth or second anterolateral tooth. Lower orbital margin (Fig. 12C) bordered by row of 13–18 small, unequal granules.

Ocular peduncle (Fig. 12A, C) reaching external orbital tooth.

Cheliped (Fig. 12E–G) generally similar to that of *I. rhizophorae*. Merus usually with distinct subdistal spine on dorsal margin. Carpus weakly elongate. Chela about 3.8 times as long as high; fixed finger weakly deflexed, cutting edge faintly dentate in proximal 0.6 and remaining distal part bordered by thin chitinous ridge; dactylus slightly curved, cutting edge faintly denticulate in proximal 0.7, bordered by thin chitinous ridge in distal 0.3.

Ambulatory legs (Fig. 9B) relatively long, slender. Fourth pereopod (third ambulatory leg) with merus 3.17–3.79 times longer than broad (n = 7, mean 3.50); propodus 4.69–6.00 times longer than broad (n = 6, mean 5.08); dactylus 0.71–0.89 times as long as propodus (n = 7, mean 0.82). Fifth pereopod (fourth ambulatory leg) with propodus 2.83–3.27 times longer than broad (n = 7, mean 3.27), outer and inner margins smooth, naked; dactylus shorter than propodus.

***Size.* –** Males cl 2.5–10.4 mm; females cl 2.8–8.5 mm, ovigerous females cl 4.0–8.5 mm.

***Colour in life.* –** Unknown.

***Distribution.* –** Vietnam, Malaysia, Singapore, Indonesia (Bintang, Sumatra and Bali), Northern Territory, Australia, New Caledonia, and Pakistan; found in mangrove, tidal flat and estuarine habitats.

***Remarks.* –** Sawada et al. (2005) presented a redescription of *Ilyograpsus paludicola*, which is accompanied by photographs of the cephalothorax of the holotype female and of a juvenile specimen collected together with the holotype. The account provides some diagnostic characters for species recognition, including the presence of a subterminal spine on the merus of the cheliped. Therefore, there was no necessity to re-examine the holotype again. The male of *Ilyograpsus paludicola* is fully described in this study for the first time.

The presence or absence of a short crest on the inner margin of the merus of the cheliped is variable in the male specimens examined. In the three smallest specimens (Bintan, Indonesia, cl 2.8, 3.1 mm, ZRC 1998.1030; Bali, Indonesia, cl 3.1 mm, CBM-ZC 9423), the crest is not differentiated. In the two specimens from Bintan (cl 3.7, 4.2 mm; ZRC 1998.1030), three specimens from Darwin Harbor, Northern Territory (cl 4.8–7.4 mm; QM W 27949) and one specimen from Cameron Beach, Northern Territory (cl 4.5 mm; QM W 19155), there is a distinct crest on the segment. In one specimen from Darwin Harbor (cl 4.6 mm; QM W 27949) and the largest specimen from Giao Thuy, Nam Dinh, Vietnam (cl 10.4 mm; CBM-ZC), there is no crest on the cheliped merus. It is apparent that the development of the crest could be variable in this species.

Ilyograpsus paludicola is morphologically closest to *I. nodulosus* and *I. daviei*, new species, and indeed there are misidentifications in previous literature of *I. paludicola* (see Synonymy). Differences between *I. paludicola* and the latter two species are discussed in detail under respective account of the two other species.

As mentioned before, the occurrence of *Ilyograpsus paludicola* in Japan has not been confirmed, although there have been supposed Japanese records of the species (Yamaguchi et al., 1976, 1987; Nakasone, 1977; Nakasone & Irei, 2003). These Japanese records are referred to *I. nodulosus*.

The presence of this species in New Caledonia has been confirmed by reexamination of the single ovigerous female specimen (OMNH-Ar 1656), which was referred to *I. paludicola* by Takeda & Nunomura (1976) and to *I. nodulosus* by Sawada et al. (2005) (see ***Remarks*** of *I. nodulosus*). This ovigerous specimen has the following features: the carapace is 1.11 times wider than long; the lower orbital margin bears 13 small granules; the merus of the cheliped is armed with a minute spine subdistally; the merus of the fourth pereopod is 3.19 times longer than wide; the dactylus of the fourth pereopod is 0.83 times as long as the propodus; and the propodus of the fifth pereopod is 3.14 times longer than wide. The size of the subdistal spine on the merus of the cheliped is much smaller in the specimen from New Caledonia than in the other specimens. Nevertheless, the specimen from New Caledonia is larger than other females specimens (cl 8.5 mm versus cl 2.8–4.6 mm), and therefore, the difference might be size-related. In other diagnostic respects, the specimen from New Caledonia well agrees with *I. paludicola*.

There have been records of *I. paludicola* from Pakistan, northern Arabian Sea, Indian Ocean (Tirmizi et al., 1985, 1986; Tirmizi & Ghani, 1996), but no specimens from the Arabian Sea were available for examination. Nevertheless, morphological features of the specimens from Pakistan seem

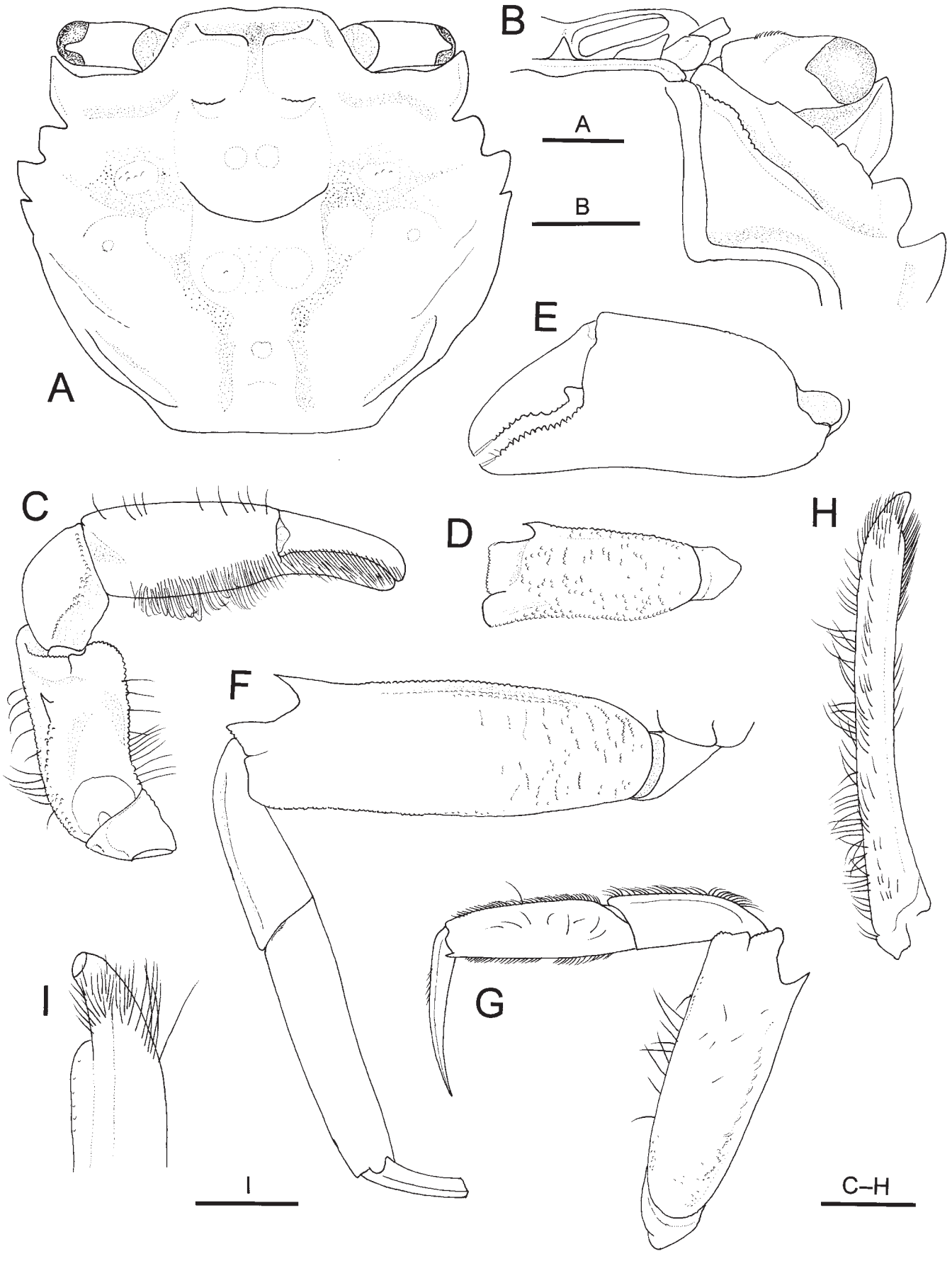

Fig. 11. *Ilyograpsus paludicola* (Rathbun, 1909). Male (cl 10.4 mm), CBM-ZC, Vietnam. A, carapace and ocular peduncles, dorsal view (setae omitted); B, left frontal to pterygostomial regions, including cephalic appendages, ventral view (setae omitted); C, left cheliped, dorsal view; D, same, merus, outer view; E, left chela, outer view; F, left fourth pereopod, dorsal view (setae omitted); G, left fifth pereopod, dorsal view; H, left first gonopod, ventrolateral view; I, same, distal part, dorsal view. Scale bars: A–H = 2 mm; H = 1 mm; I = 0.5 mm.

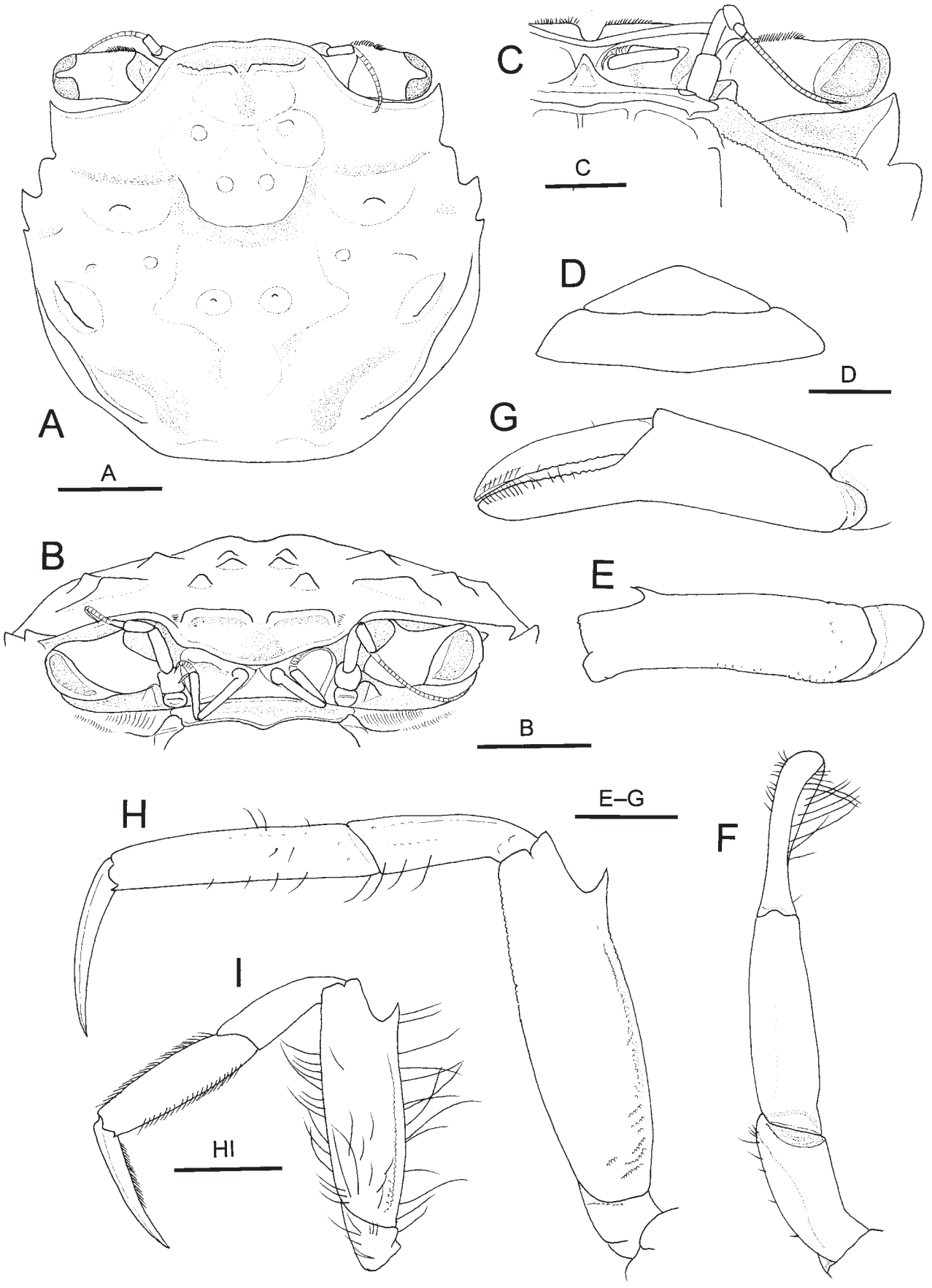

Fig. 12. *Ilyograpsus paludicola* (Rathbun, 1909). Ovigerous female (cl 8.0 mm), ZRC 1998-1030, Bintan, Indonesia. A, carapace, ocular peduncles and antennae, dorsal view (setae omitted); B, cephalothorax and cephalic appendages, frontal view; C, left frontal to pterygostomial regions, including cephalic appendages, ventral view; D, sixth pleonal somite and telson, ventral view; E, merus of left cheliped, outer view; F, carpus and chela of left cheliped, dorsal view; G, left chela, outer view; H, left fourth pereopod, dorsal view; I, left fifth pereopod, dorsal view. Scale bars: A, B, D, H, I = 2 mm; C, E–G = 1 mm.

to agree with the present specimens in every diagnostic aspect. The occurrence of *I. paludicola* from the western Indian Ocean and the Red Sea has not been confirmed.

Ilyograpsus daviei, new species
(Figs. 13–15)

Ilyograpsus paludicola — Davie, 2002: 229 (in part).
Ilyograpsus nodulosus — Sawada et al., 2005: 857 (in part).

Material examined. – Holotype - male (cl 7.3 mm), QM W 15556a, Boggy Creek, Myrtletown, Brisbane, Queensland, 27°24'S 153°08'E, under rocks near low tide mark, 12 Jul.1998, coll. J. Short et al.

Paratypes: 1 ovigerous female (cl 10.2 mm), QM W 5265, Jackson Creek, Queensland, 12 Oct.1972, coll. B. M. Campbell; 3 males (cl 5.0–7.0 mm), 1 female (cl 6.1 mm), 8 ovigerous females (cl 6.0–8.0 mm), QM W 15554a, Boggy Creek, Myrtletown, Brisbane, Queensland, burrows in mud bank, 12 Jul.1988, coll. J. Short; 1 male (cl 5.2 mm), 1 ovigerous female (cl 8.4 mm), QM W 15556b, same data as holotype; 1 male (cl 6.3 mm), 1 ovigerous female (cl 8.3 mm), QM W 23889, same locality, estuarine, littoral, 29 Jul.1997, coll. P. Davie & J. Short.

Non-type: 2 young males (cl 3.3, 3.3 mm), 1 female (damaged), QM W 15554b, Boggy Creek, Myrtletown, southeast Queensland, in burrows in mud bank, coll. J. Short et al.

Description of male. – Carapace (Fig. 14A, B) suboctogonal, breadth 1.12–1.19 times length (n = 6, mean 1.15); regions relatively weakly defined. Postfrontal ridges distinct, separated by broad median sulcus. Epigastric ridges or tubercles present. Cardiac region with paired low elevations; branchial regions with 1 or 2 pairs of low elevations on either side of gastro-cardiac region, and with few short longitudinal ridges laterally. Lateral margins generally convex, greatest carapace breadth between third anterolateral teeth. Four anterolateral teeth present, first tooth (external orbital tooth) largest, triangular, acute or subacute; second tooth slightly exceeding external orbital tooth, rounded or bluntly triangular; third tooth clearly exceeding beyond external orbital tooth or second anterolateral tooth, varying from blunt to acute; fourth tooth small, but clearly delineated, blunt or subacute. Front distinctly less than posterior width, about 0.4 times front-orbital width, wider than orbit; anterior edge in dorsal view faintly bilobed. Upper orbital margin concave or slightly sinuous, almost transverse; lower orbital margin (Fig. 14C) with 3–5 lobules laterally.

Ocular peduncle (Fig. 14A) reaching or slightly falling short of external orbital tooth, length about 2.0–2.3 of corneal width; cornea not dilated.

Cheliped (Fig. 14E–H) of larger males (cl 5.2–7.3 mm) with merus bearing small subdistal spine on dorsal margin and distinct crest on anterior surface adjacent to inner margin. Chela about 1.80–2.00 times as long as high; ventral margin faintly sinuous; inner surface of palm with covering of dense setae extending onto fingers; fingers leaving proximal hiatus when closed; fixed finger not deflexed, cutting edge with row of small, blunt teeth almost over entire length, distal part bordered by thin chitinous ridge. Dactylus nearly straight, subequal in length to palm, cutting edge with low molar-like tooth proximal to midlength, otherwise weakly dentate, distal part bordered by chitinous ridge.

Cheliped of smaller males (cl 3.3–5.0 mm) similar to that of *I. paludicola*.

Ambulatory legs (Fig. 13A) relatively short, stout. Meri broadened distally, each with relatively large subdistal spine. Fourth pereopod (third ambulatory leg) (Fig. 14I) with merus about 2.47–3.02 times longer than broad (n = 5, mean 2.88), anterior margin slightly sinuous, posterior margin slightly convex; propodus 3.27–3.58 times longer than broad (n = 5, mean 3.44); dactylus 0.64–0.87 times as long as propodus (n = 5, mean 0.80). Fifth pereopod (fourth ambulatory leg) (Fig. 14J) with propodus 2.00–2.87 times longer than broad (n = 5, mean 2.43), outer and inner margins fringed with short setae; dactylus subequal to or slightly longer than propodus.

Sixth pleonal somite (Fig. 14D) with straight or faintly sinuous lateral margins, about 2.5–2.7 times broader than long. Telson rounded terminally; breadth about 1.1–1.2 times length.

First gonopod (Fig. 14K) moderately slender, very slightly curved; terminal process (Fig. 14L) moderately long, slightly curved dorsally, partially obscured by numerous stiff setae; subterminal lobe not delineated.

Description of female. – Carapace (Fig. 15A) generally similar to that of male; breadth about 1.15–1.21 times length (n = 11, mean 1.19); greatest carapace breadth between

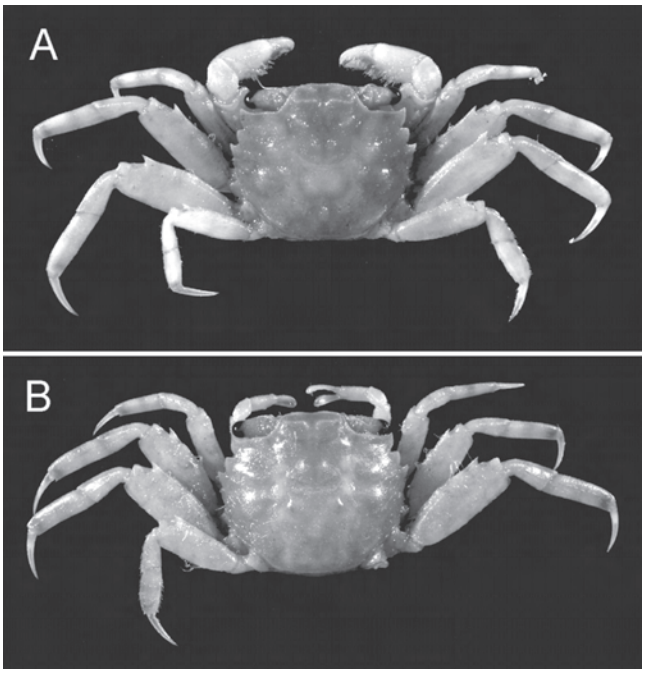

Fig. 13. *Ilyograpsus daviei*, new species. Entire animals in dorsal view. A, male (cl 7.3 mm), holotype, QM W 15556, Boggy Creek, Myrtletown, Brisbane, Queensland, Australia; B, female (cl mm), paratype, QM 15554, same locality.

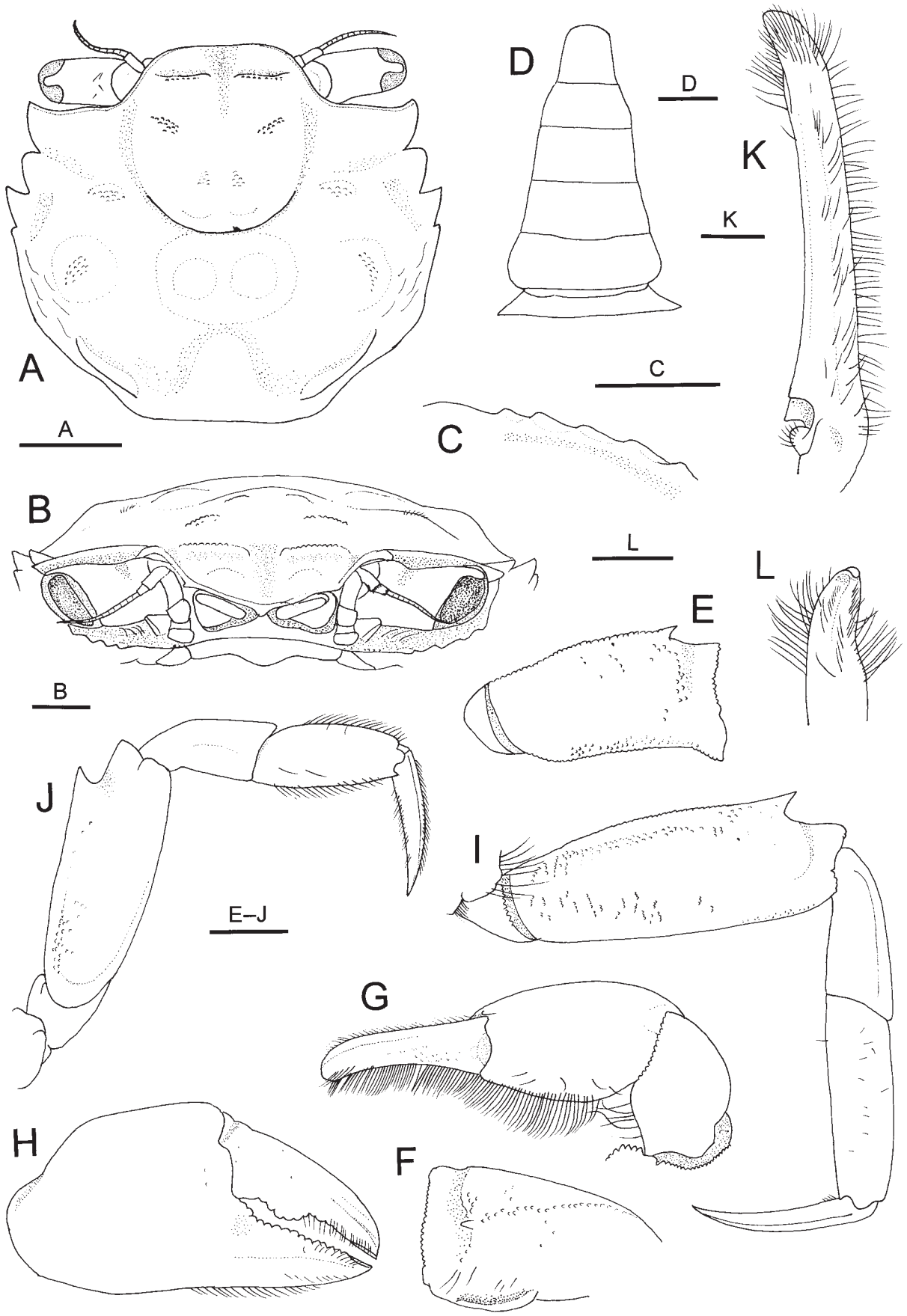

Fig. 14. *Ilyograpsus daviei*, new species. Holotype, male (cl 7.3 mm), QM W 15556, Boggy Creek, Myrtletown, Brisbane, Queensland, Australia. A, carapace, ocular peduncles and antennae, dorsal view (setae omitted); B, cephalothorax and cephalic appendages, frontal view; C, left lower orbital margin, ventral view; D, pleon, ventral view; E, merus of right cheliped, outer view; F, same, dorsal view; G, carpus and chela of right cheliped, dorsal view; H, right chela, outer view; I, right fourth pereopod, dorsal view; J, right fifth pereopod, dorsal view; K, left first gonopod, ventral view;; L, same, distal part, dorsal view. Scale bars: A, B, E–I = 2 mm; C, D = 1 mm; K, L = 0.5 mm.

third anterolateral teeth. Third anterolateral tooth exceeding beyond external orbital tooth or second anterolateral tooth. Lower orbital margin (Fig. 15B) bordered by row of 13–18 small granules becoming larger and more widely spaced laterally.

Pleon and telson (Fig. 15) similar to those of other congeneric species.

Merus of cheliped (Fig. 15D) with distinct subdistal spine on dorsal margin. Chela (Fig. 15E) with fixed finger slightly deflexed, cutting edge not dentate; dactylus with nearly smooth cutting edge.

Ambulatory legs similar to those of males; meri broadened distally. Fourth pereopod with merus 2.24–2.77 times longer than broad (n = 10, mean 2.56); propodus 3.18–3.85 times

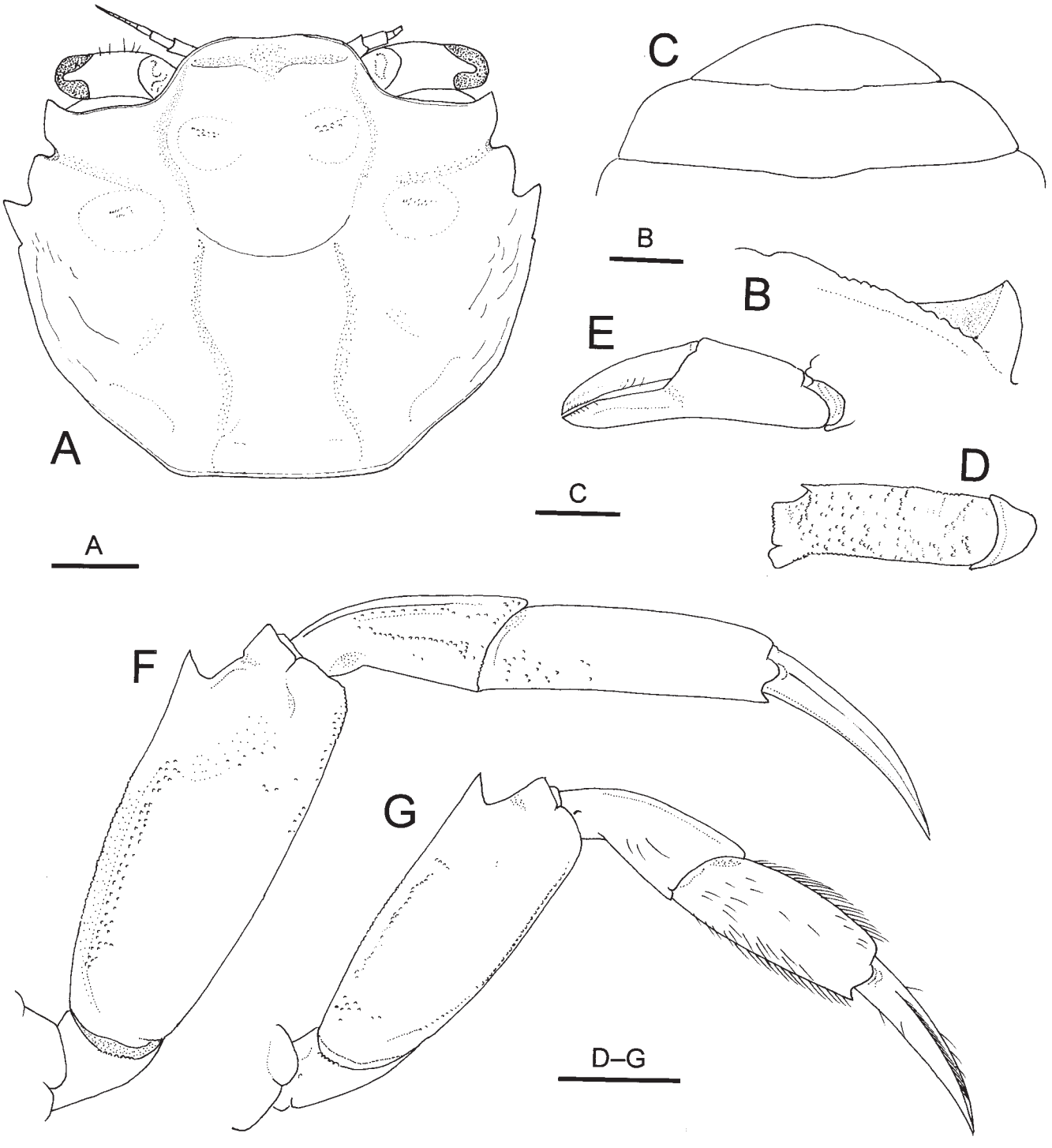

Fig. 15. *Ilyograpsus daviei*, new species. Paratype, female (cl 7.3 mm), QM W 5265, Queensland, Australia. A, carapace, ocular peduncles and antennae, dorsal view; B, left lower orbital margin and external orbital tooth, ventral view; C, sixth pleonal somite and telson, ventral view; D, merus of left cheliped, outer view; E, left chela, outer view; F, right fourth pereopod, dorsal view (setae omitted); G, right fifth pereopod, dorsal view. Scale bars: A, C, E–G = 2 mm; B = 1 mm.

longer than broad (n = 10. mean 3.41); dactylus 0.72–0.86 times as long as propodus (n = 10, mean 0.80). Fifth pereopod with propodus 2.05–2.45 times longer than broad (n = 9, mean 2.09); dactylus subequal to or slightly longer than propodus.

***Size*. –** Males cl 5.0–7.3 mm; females cl 6.0–10.2 mm, ovigerous females cl 6.0–10.0 mm.

***Distribution*. –** Known with certainty only from Queensland, Australia.

***Remarks*. –** The present new species is similar to *I. paludicola* and *I. nodulosus* particularly in the general shape of the carapace. Nevertheless, *I. daviei* is differentiated from the latter two species by the less clearly defined carapace regions and the distinctly stouter ambulatory legs (Table 1). Particularly, the fifth pereopod is relatively stout in the new species. From *I. nodulosus*, *I. daviei* can be separated further by the different ornamentation of the lower orbital margin in females, the merus of the cheliped with a subdistal spine on the dorsal margin and with a short subdistal crest on the anteroventral margin, and the more elongate terminal process of the first gonopod.

The material referred to *I. nodulosus* by Sawada et al. (2005) contains specimens from Brisbane, Queensland, where the occurrence of the present new species has been confirmed. We consider that the specimens used by Sawada et al. (2005) could be referred to *I. daviei*, and thus the reference is included in the synonymy of the present new species.

***Etymology*. –** The new species is named in honour of our esteemed colleague, Peter J. F. Davie of the Queensland Museum, in recognition of his great contributions to the systematics of the Decapod Crustacea in the Indo-Pacific region.

Apograpsus, new genus

***Type species*. –** *Ilyograpsus paantu* Naruse & Kishino, 2006. Present designation by monotypy. Gender: masculine.

***Diagnosis*. –** Carapace (Figs. 17A, B; 18A) longer than wide; regions on dorsal surface well defined with gastric, cardiac, intestinal regions markedly elevated; cardiac region with 2 rounded prominences; intestinal region with low median ridge; lateral margin with 3 teeth including external orbital tooth, of which second tooth rudimentary; margin between external orbital tooth and third lateral tooth concave, thus carapace weakly constricted. Front broad, markedly bilobed, not constricted at base. Postfrontal ridges longitudinal, with few long setae anteriorly. Orbit large; upper orbital margin oblique; lower orbital margin (Fig. 17C) fairly oblique, smooth or faintly granular, mesial angle produced into prominent projection; inner orbital tooth small. Ocular peduncle (Figs. 17A, B; 18A) slightly constricted; cornea large. Antennules (Fig. 17B) transverse or slightly oblique; basal segment inflated; inter-antennular septum narrow. Antennae (Fig. 17B) in orbital hiatus; flagellum relatively long. Central region of epistome strongly convex (Fig. 17B). Third maxilliped (Fig. 17E) similar to that of *Ilyograpsus*. Cheliped (Figs. 16A, B; 17G; 18C, D) small in male and female; merus (Figs. 17F; 18B) narrowed distally, without subdistal spine on dorsal margin; carpus without prominent tooth or spine on inner surface; dactylus without differentiated teeth on cutting edges in male; fingers spoon-shaped at tips, not crossing when closed. Ambulatory legs (Fig. 16A, B) slender; meri (Figs. 17I, J; 18E, F) each with sharp subdistal spine on anterior margin; propodi unarmed at posterodistal angles. Pleon generally similar to that of *Ilyograpsus*; first somite with rounded lateral margin in male (Fig. 17D). First gonopod (Fig. 17H) stout, nearly straight in ventral view, slightly constricted at midlength; terminal process (Fig. 17I) very short, roundly truncate. Female gonopores close to suture between fifth and sixth sternite.

***Remarks*. –** As already noted by Naruse & Kishino (2006), this species markedly differs from other species of *Ilyograpsus* in many characters. In particular, the carapace being longer than broad, the longitudinal postfrontal ridges with peculiar long setae anteriorly, the conspicuously projecting anteromesial angle of the lower orbital margin and the slightly constricted male first gonopod are unique for *Apograpsus*. In *Ilyograpsus*, the carapace is wider than long; the postfrontal ridges are transverse with procurved lateral parts; no setae is present at the anterolateral angle of the front; the anteromesial angle of the lower orbital margin is not markedly produced; and the first gonopod is not constricted at the middle. Furthermore, *Apograpsus* differs from *Ilyograpsus* in having three anterolateral teeth on the carapace, of which the second is rather obsolete. In *Ilyograpsus*, there are four anterolateral teeth. The meri of third and fourth pereopods in females (second and third ambulatory legs) are narrowed distally in *Apograpsus*, but in *Ilyograpsus*, the meri of these legs are not narrowed. The sister group of *Apograpsus* is still unclear, although the structure of the front and orbit of the carapace and the armature of the ambulatory meri link *Apograpsus* to *Ilyograpsus*, *Enigmaplax* and the hypothetical ancestor of *Macrophthalmus* (see Barnes, 1967). It is interesting to note that juveniles of *Ilyograpsus* species show some superficial resemblance to *Apograpsus paantu*, particularly in the carapace shape and the development of the anterolateral teeth (see Sawada et al., 2005, Fig. 4B). This would seem to suggest a possibility that *Apograpsus paantu* was perhaps derived through a process of neoteny.

***Etymology*. –** The name is derived from the Greek prefix "*Apo*-", meaning remote, in arbitrary combination with the genus name "*Grapsus*", in reference to the non-close relationship of the type species and closely related *Ilyograpsus* species to the Grapsidae or other related families.

Apograpsus paantu (Naruse & Kishino, 2006), new combination
(Figs. 16–18)

Ilyograpsus paantu Naruse & Kishino, 2006: 68, Figs. 2a, 3, 4.

***Name bearing type.* –** Holotype: male (cl 3.4 mm), RUMF-ZC-237, Tima River, Nago, Okinawa Island, 13 Feb.2005, coll. T. Naruse.

***Material examined.* –** Holotype (see above). Paratypes - 1 male (cl 3.4 mm), 2 females (cl 4.7, 5.8 mm), 3 ovigerous females (cl 4.7–5.6 mm), RUMF-ZC-238, same data as holotype; 1 female (cl 5.4 mm), CBM-ZC 8492, Atetsu River estuary, Amami-oshima Island, 4 Aug.2000, coll. Y. Yonezawa; 1 ovigerous female (cl 6.4 mm), CBM-ZC 8493, Yanma, Sumiyo Village, Amami-oshima Island, 31 Mar.2002, coll. T. Kishino; 1 male (cl 3.9 mm), 1 female (cl 6.1 mm), CBM-ZC 8834, Yagaji Port, Yagaji Island, Okinawa Islands, 1.5 m, coll. T. Komai, 17 Mar.2006; 2 females (cl 3.3, 3.3 mm), CBM-ZC, Sonai Port, Iriomote Island, Yaeyama Islands, 2 m, 29 Jun.2005, mooring rope, coll. T. Komai.

***Diagnosis.* –** See generic diagnosis given above. Detailed description and illustrations is given by Naruse & Kishino (2006).

***Size.* –** Males cl 3.4–3.9 mm; females cl 3.3–6.4 mm, ovigerous females cl 4.7–6.4 mm.

***Distribution and habitat.* –** Known only from the Ryukyu Islands of southern Japan: Amami-ohshima Island, Okinawa Islands, and Iriomote Island. According to Naruse & Kishino (2006), the type specimens were collected from riverbeds of brackish waters, with a pebbly-muddy substratum. The newly obtained specimens were collected from small fishing ports facing sea shore, with a muddy substratum. It is suggested that the species is fairly tolerant against changes of salinity.

***Remarks.* –** Like species of *Ilyograpsus*, *Apograpsus paantu* shows notable sexual dimorphism in some characters. For example, the external orbital teeth are more strongly projecting in males than in females (cf. Figs. 17A and 18A); the ocular peduncles is relatively larger in males than in females (cf. Figs. 17A and 18A); the front is more distinctly bilobed in males than in females (cf. Figs. 17A and 18A); the ambulatory legs are shorter in females than in males (cf. Fig. 16A and 16B). On the other hand, the structure of the lower orbital margin is similar between males and females.

BIOGEOGRAPHY

So far, species of *Ilyograpsus* are known only from the Indo-West Pacific region, although geographical ranges of all but *I. paludicola* appears rather limited. *Ilyograpsus paludicola* is rather widespread in the western Pacific including Vietnam, Thailand, Malaysia, Singapore, Indonesia, northern to northeastern Australia and New Caledonia, and Pakistan in the northern Arabian Sea, Indian Ocean. On the other hand, two species, *I. rhizophorae* and *I. vannini*, occur in the western Indian Ocean, and the former extends to the Red Sea. *Ilyograpsus daviei* is perhaps endemic to eastern Australia, because the known specimens all came from Queensland. *Ilyograpsus nodulosus* appears restricted to southwestern part of the Japanese Archipelago, extending to temperate regions (i.e., Seto Inland Sea and Wakayama Prefecture). It is possible that *I. daviei*, new species, and *I. nodulosus* were derived by isolation of peripheral populations of *I. paludicola* or common ancestor of the three taxa. *Apograpsus paantu* is known only from the Ryukyu Islands in southwestern Japan. Collections of species of *Ilyograpsus* and *Apograpsus* are still rather scarce, and further study is needed to document real distributional pattern of each species.

Key to species of *Ilyograpsus* and *Apograpsus*, new genus

1. Carapace longer than broad, with 3 anterolateral teeth (including external orbital tooth) of which second tooth poorly developed; postfrontal ridges longitudinal, each with peculiar long setae anteriorly ..... *Apograpsus paantu*, new combination
– Carapace wider than long, with 4 conspicuous anterolateral teeth (including external orbital tooth); postfrontal ridges transverse or L-shaped, without long setae ..... 2 (*Ilyograpsus*)
2. Regions of carapace poorly defined, lacking epigastric ridges or tubercles 3
– Regions of carapace markedly defined, bearing epigastric ridges or tubercles 4
3. Second and third anterolateral teeth moderately large, anterolateral margin generally convex; male first gonopod with elongate terminal process ..... *Ilyograpsus rhizophorae*
– Second and third anterolateral teeth small, anterolateral margin nearly parallel; male unknown ..... *I. vannini*
4. Merus of cheliped with conspicuous subdistal spine; proportional length of dactylus of fourth pereopod (length of dactylus / length of propodus) included in range of 0.60–0.90; terminal process of male first gonopod somewhat elongate 5

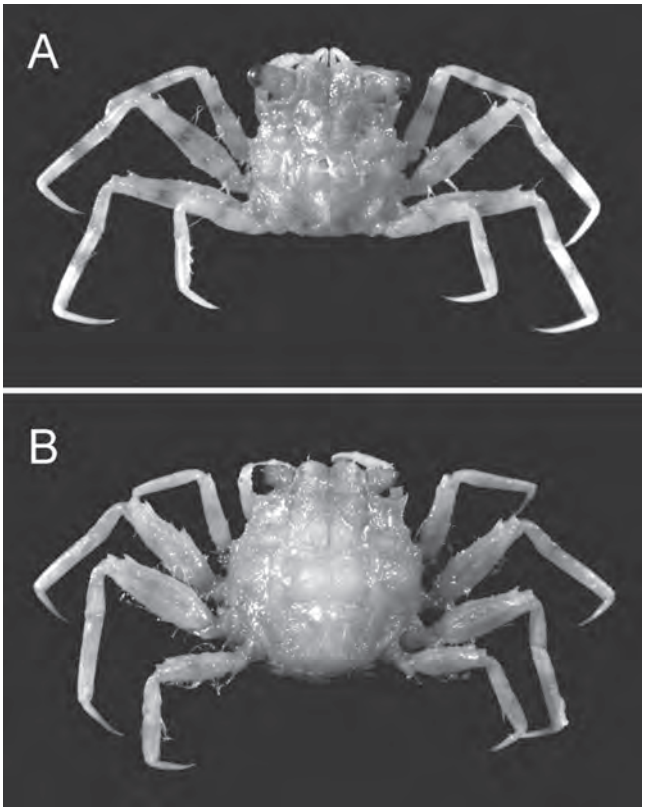

Fig. 16. *Apograpsus paantu* (Naruse & Kishino, 2006), new combination. A, male (cl 3.4 mm), RUMF-ZC-238, paratype, Tima River estuary, Nago, Okinawa Island, Japan; B, female (cl 6.4 mm), paratype, CBM-ZC 8493, Yanma, Sumiyo, Amami-ohshima Island, Japan.

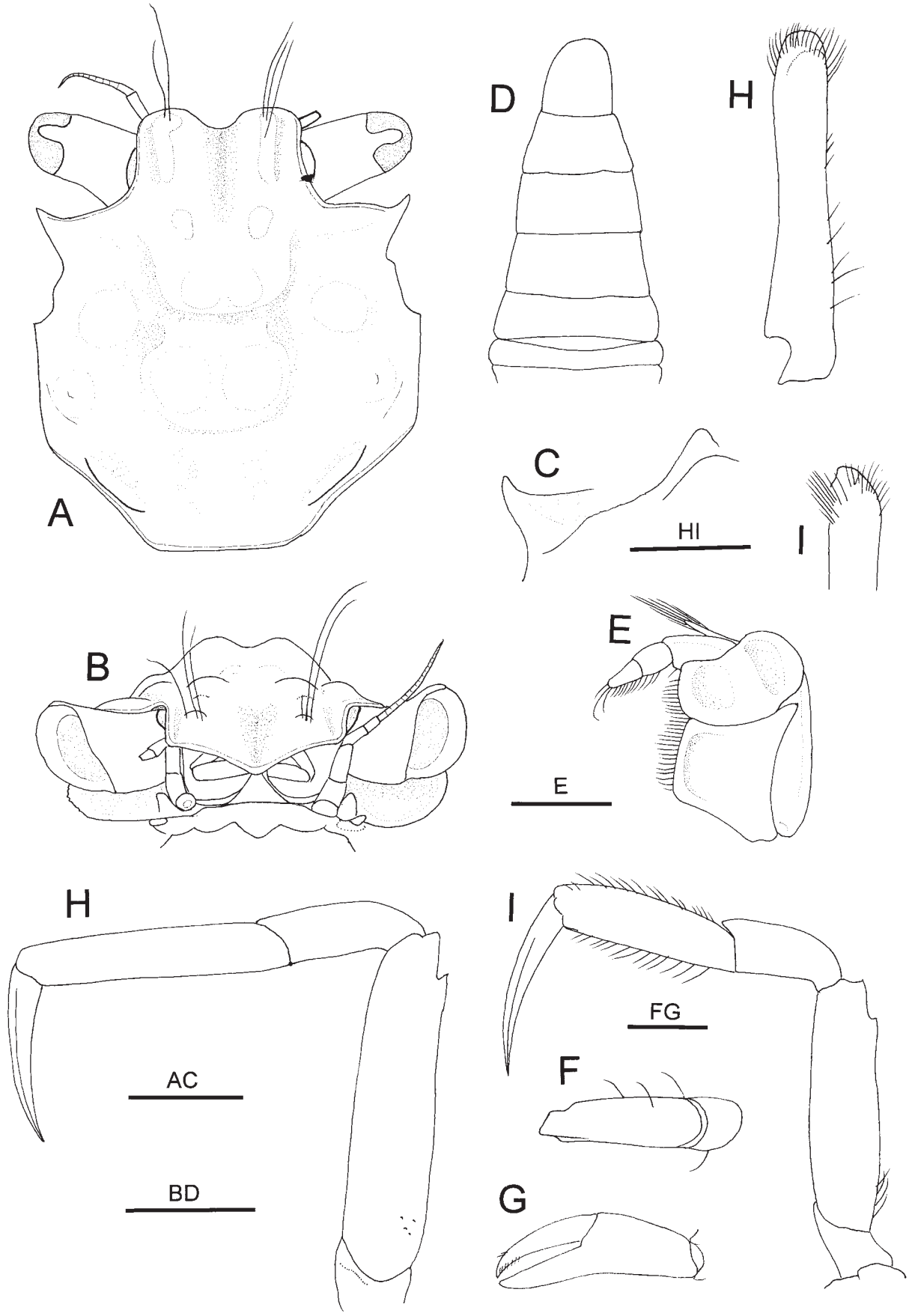

Fig. 17. *Apograpsus paantu* (Naruse & Kishino, 2006), new combination. A–E, H, I, male (cl 3.9 mm), CBM-ZC 8834, Yagaji Port, Yagaji Island, Okinawa Islands, Japan. F, G, male (cl 3.4 mm), paratype, RUMF-ZC-238, Tima River estuary, Nago, Okinawa Island. A, carapace, ocular peduncles, and antennae, dorsal view (setae partially omitted); B, cephalothorax and cephalic appendages, frontal view; C, right lower orbital margin, ventral view; D, pleon, ventral view; E, left third maxilliped, ventral view; F, left fourth pereopod, dorsal view; G, left fifth pereopod, dorsal view; H, left first gonopod, ventral view; I, same, distal part, dorsal view. Scale bars: A, B, D = 1 mm; E–I = 0.5 mm.

– Merus of cheliped unarmed or with minute granules or tubercles subdistally; proportional length of dactylus of fourth pereopod (length of dactylus/length of propodus) included in range of 0.85–1.05; terminal process of first gonopod very short, truncate ..... *I. nodulosus*

5. Ambulatory legs slender, propodus of fifth pereopod more than 3.0 times longer than wide in males and more than 2.5 times in females ..... *I. paludicola*
– Ambulatory legs stout, propodus of fifth pereopod less than 3.0 times longer than wide in males, less than 2.5 times in females ..... *I. daviei*, new species

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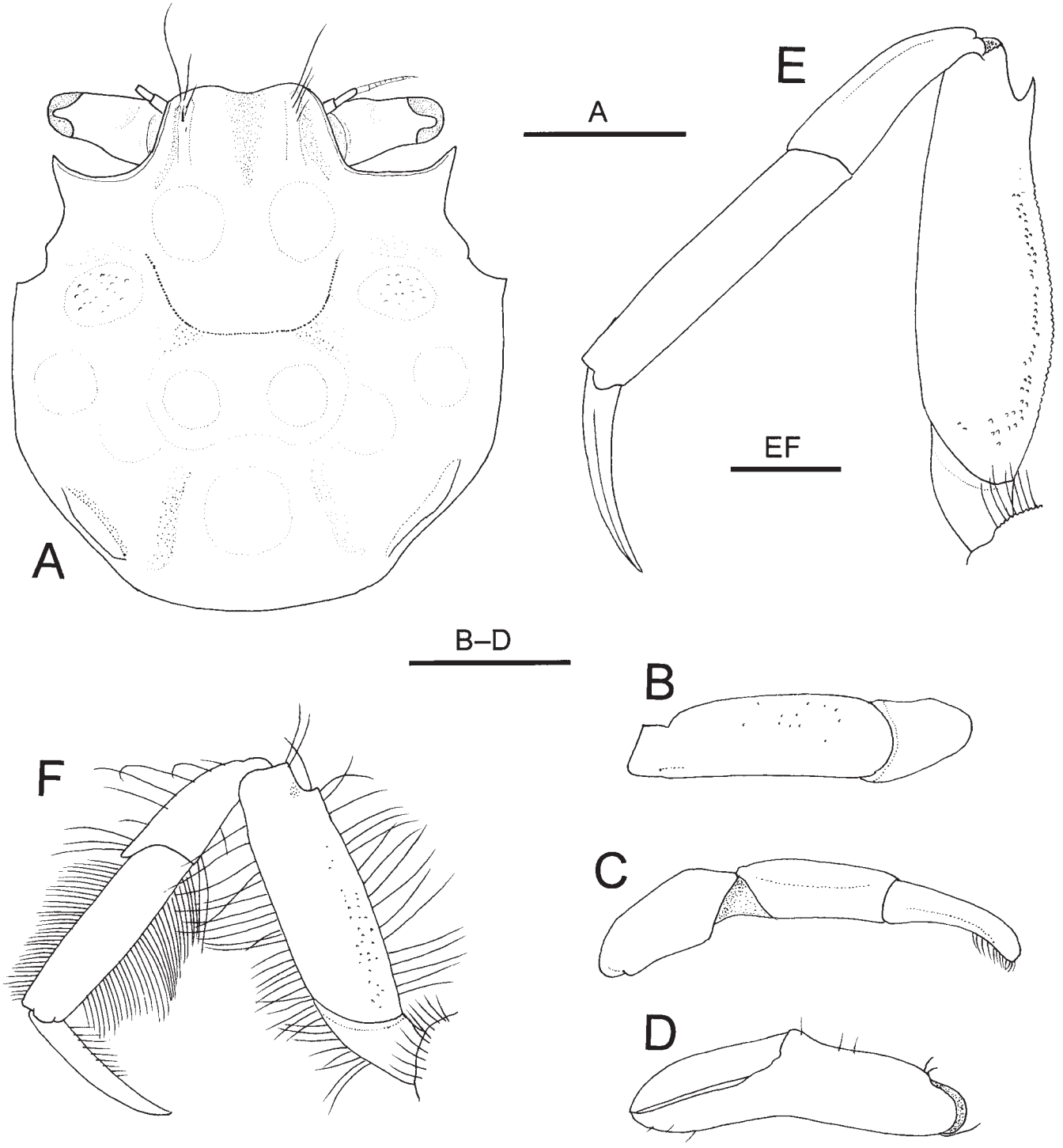

Fig. 18. *Apograpsus paantu* (Naruse & Kishino, 2006), new combination. Female (cl 6.4 mm), paratype, CBM-ZC 8493, Yanma, Sumiyo, Amami-ohshima Island, Japan. A, carapace, ocular peduncles and antennae, dorsal view; B, merus of left cheliped, outer view; C, chela and carpus of left cheliped, dorsal view; D, left chela, outer view; E, left fourth pereopod, dorsal view; F, left fifth pereopod, dorsal view. Scale bars: A = 2 mm; B–F = 1 mm.

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LITERATURE CITED

Barnard, K. H., 1955. Addition to the fauna-list of South African Crustacea and Pycnogonida. *Annals of the South African Museum*, **43**: 1–107, pl. 1.

Barnes, R. S. K., 1966. The status of the genus *Euplax* H. Milne Edwards, 1852; and a new genus *Australoplax* of the subfamily Macrophthaminae Dana, 1851 (Brachyura, Ocypodidae). *Australian Zoologist*, **13**: 370–376.

Barnes, R. S. K., 1967. The Macrophthalminae of Australasia; with a review of the evolution and morphological diversity of the type genus *Macrophthalmus*. *Transactions of the Zoological Society of London*, **31**: 195–262.

Barnes, R. S. K., 1977. Concluding contribution towards a revision of, and a key to, the genus *Macrophthalmus* (Crustacea: Brachyura). *Journal of Zoology, London*, **182**: 267–280.

Crosnier, A., 1965. Crustacés Décapodes, Grapsidae et Ocypodidae. *Faune de Madagascar*, **18**: 1–143, Pls. 1–11.

Cuesta, J. A., J. I. González-Gordillo & A. Rodríguez, 1997. First zoeal stages of *Grapsus adscensionis* (Osbeck) and *Planes minutus* (Linnaeus) (Brachyura: Grapsidae) described from laboratory hatched material, with notes on larval characters of the Grapsinae. *Journal of Natural History*, **31**: 887–900.

Dana, J. 1851. On the classification of the Crustacea Grapsoidea. *American Journal of Science and Arts*, (2)**12**: 283–291.

Davie, P. J. F., 1993. A new genus of macrophthalmine crab (Crustacea: Decapoda: Ocypodidae) from eastern Australia. *Records of the Australian Museum*, **45**: 5–9.

Davie, P. J. F., 2002. *Crustacea: Malacostraca: Eucarida (Part 2): Decapoda—Anomura, Brachyura*. In: Wells, A. & W. W. K. Houston (eds.) *Zoological Catalogue of Australia*. Vol. 19.3B. CSIRO Publishing, Melbourne. Pp. xiv+641.

Desmarest, A. G., 1822. Histoire d'Crustacés fossilles. In: *Dictionnaire des Sciences Naturelles*. F. G. Levreault, Paris. Pp. 67–142.

Desmarest, A. G., 1823. Malacostracés. In: *Dictionnaire des Sciences Naturelleles*, Vol. 28. F. G. Levreault, Paris. Pp. 138–425.

Fishelson, L., 1971. Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. *Marine Biology*, **10**: 113–133.

Flores, A. A., J. Paula & T. Dray, 2003. First zoeal stages of grapsoid crabs (Crustacea: Brachyura) from the East African coast. *Zoological Journal of the Linnean Society, London*, **137**: 355–383.

Fukuda, Y., 1978. Preliminary notes on recently obtained larvae of brachyuran Crustacea of the sea around Aitsu Marine Biological Station. *Calanus*, **6**: 10–16. [in Japanese with English abstract]

Hartnoll, R. G., 1975. The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *Journal of Zoology, London*, **177**: 305–328.

Holthuis, L. B., 1977. The Grapsidae, Gecarcinidae and Palicidae (Crustacea: Decapoda: Brachyura) of the Red Sea. *Israel Journal of Zoology*, **26**: 142–192.

Kensley, B., 1981. On the zoogeography of southern African decapod Crustacea, with a distributional checklist of the species. *Smithsonian Contributions to Zoology*, **338**: i–iii, 1–64.

Kishino, T., A. Nomoto, S. Kimura, T. Yonezawa & K. Wada, 2001a. Brachyuran crab species recorded in the brackish waters of Amami-Oshima Island, Kagoshima Prefecture, Japan. *Nankiseibutsu*, **43**: 125–131. [in Japanese with English abstract]

Kishino, T., T. Yonezawa, A. Nomoto, S. Kimura & K. Wada, 2001b. Twelve rare species of brachyuran crabs recorded in the brackish waters of Amami-Oshima Island, Kagoshima Prefecture, Japan. *Nankiseibutsu*, **43**: 15–12.

Kitaura, J., K. Wada & M. Nishida, 2002. Molecular phylogeny of grapsoid and ocypodoid crabs with special reference to the genera *Metaplax* and *Macrophthalmus*. *Journal of Crustacean Biology*, **22**: 682–693.

Milne Edwards, H., 1852. Observations sur le affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences naturelles*, (3)**18**: 109–166, pls. 3, 4.

Nakasone, Y., 1977. Crab zonation in the Yuhi River, Okinawa Island. *Japanese Journal of Ecology*, 27: 61–70.

Nakasone, Y. & M. Irei, 2003. Grapsidae. In: M. Nishida, N. Shikatani & S. Shokita (eds.), *The flora and fauna of inland waters in the Ryukyu Islands*. Tokai University Press, Tokyo. Pp. 272–282. [in Japanese]

Naruse, T., 2005. *Ilyograpsus nodulosus*. In: Nature Conservation Division, Department of Cultural and Environmental Affairs, Okinawa Prefecture (ed.) *Threatened Wildlife in Okinawa, Second Edition (Animals). Red Data Okinawa*. Okinawa Prefectural Government, Naha. Pp. 1–221. [in Japanese]

Naruse, T. &. T. Kishino, 2006. New species of *Ilyograpsus* from the Ryukyu Islands, Japan, with notes on *I. nodulosus* Sakai, 1983. *Crustacean Research*, **35**: 67–78.

Ng, P. K. L., D. Guinot & P. J. F. Davie, 2008. Systema Brachyurorum: Part 1. An annotated check list of extant brachyuran crabs of the world. *The Raffles Bulletin of Zoology*, 17: 1–286.

Rafinesque, C. S., 1815. *Analyse de la nature ou tableau de l'univers et de corps organisés*. Palermo, pp. 224. [not seen]

Rathbun, M. J., 1909. New crabs from the Gulf of Siam. *Proceedings of the Biological Society of Washington*, **22**: 107–114.

Rathbun, M. J., 1910. The Danish expeditions to Siam 1899–1900. V. Brachyura. *Kongelige Danske Videnskabernes Selskabs Skrifter, Kovenhavn*, (7) **5**: 301–367, Pls. 1, 2.

Sakai, T., 1983. Descriptions of new genera and species of Japanese crabs, together with systematically and biogeographically interesting species. (I). *Researches on Crustacea*, **12**: 1–44, Pls. 1–8, 1 frontispiece.

Sawada, T., M. Hosogi & K. Sakai, 2005. A new species of the genus *Ilyograpsus*, *I. vannini* sp. nov. (Brachyura, Grapsidae) from Somalia. *Crustaceana*, **78**: 851–864.

Schubart, C. D., S. Cannici, M. Vannini & S. Fratini, 2006. Molecular phylogeny of grapsoid crabs (Decapoda, Brachyura) and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. *Journal of Zoological Systematics and Evolutionary Research*, **44**: 193–199.

Serène, R., 1971. Observations préliminaires sur des brachyoures nouveaux ou mal connus du sud-est Asiatique (Crustacea Decapoda). *Bulletin du Muséum national d'Histoire naturelle*, (2) **42**: 903–918.

Shen, C.-J., 1935. On some new and rare crabs of the families Pinnotheridae, Grapsidae and Ocypodidae from China. *Chinese Journal of Zoology*, **1**: 19–40.

Števčić, Z., 2005. The reclassification of Brachyuran crabs (Crustacea: Decapoda: Brachyura). *Fauna Croatica*, **14**(1): 1–159.

Stimpson, W., 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missam Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit, Pars V. Crustacea Ocypodoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1858: 93–110.

Takeda, M. & N. Nunomura, 1976. Crabs collected by the Melanesia Expedition of the Osaka Museum of Natural History, 1958. *Bulletin of the Osaka Museum of Natural History*, **30**: 61–92.

Tan, C. G. S. & P. K. L. Ng. 1999. A revision of the genus *Camptandrium* Stimpson, 1858 (Crustacea: Decapoda: Brachyura: Camptandriidae). *The Raffles Bulletin of Zoology*, **47**: 193–219.

Tesch, J. J., 1918. The Decapoda Brachyura of the Siboga Expedition, I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga-Expeditie*, **39c**: 1–148, Pls. 1–6.

Tirmizi, N. M. & N. Ghani, 1996. Marine fauna of Pakistan: 5. Crustacea: Brachyura, Brachyrhyncha Part I (Xanthidae, Goneplacidae, Pinnotheridae, Ocypodidae, Grapsidae). Centre of Excellence in Marine Biology, University of Karachi, Karachi. 188 pp.

Tirmizi, N. M., Q. B. Kazmi & N. Ghani, 1985. Five brachyuran crabs new to the northern Arabian Sea (Karachi). *Pakistan Journal of Zoology*, **17**; 21–27.

Vannini, M. & P. Valmori, 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 30. Grapsidae (Decapoda Brachyura). *Monitore Zoologico Italiano*, New Series, Supplement, **14**: 57–101.

Yamaguchi, T., M. Takeda & K. Tokutome, 1976. A list of crabs collected in the vicinity of the Aitsu Marine Biological Station and a preliminary report on the cheliped asymmetry of the crabs. *Calanus*, **5**: 31–46. [in Japanese]

Yamaguchi, T., K. Harada, M. Takeda & T. Kikuchi, 1987. Crab fauna of the Amakusa Islands. *Calanus*, **10**: 1–71. [in Japanese with English abstract]

Yeo, D. C., D. L. Rahayu & P. K. L. Ng, 2004. Brachyura (Crustacea) of the Anambas Expedition 2002. *Raffles Bulletin of Zoology*, Supplement, **11**: 79–88.